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A new phylogeny of ichthyosaurs (Reptilia: Diapsida)

Benjamin C. Moon^{*a}

^a *Palaeobiology Research Group, School of Earth Sciences, University of Bristol, 24 Tyndall Avenue, Bristol BS8 1TQ, United Kingdom*

Abstract

The largest phylogenetic analysis of ichthyosaurs to date is presented, with 114 ingroup taxa coded at species level. Completeness of the taxa included varied from >98% to <2%; ten taxa were removed *a priori* using Concatanabominations, due to incompleteness and taxonomic uncertainty. The data were analysed using three widely used optimisation criteria: maximum parsimony, maximum likelihood, and Bayesian inference; while similar, each criterion produced different topologies, support, and levels of resolution. Maximum parsimony found a well-resolved consensus tree with minor improvement from *a posteriori* pruning of unstable taxa; however, general support remains low. Tree resolution was reduced more by taxa that lacked codings from phylogenetically important regions of the tree, rather than by those that simply lacked many codings. Resolution present in the most likely tree is poorly supported; sister relationships cannot be confirmed, although similarities are found to the most parsimonious tree. Bayesian inference found poorly resolved consensus trees. While more resolved, an equal-distribution rate prior is significantly worse than the null gamma-distribution rate prior for morphological data, but suggests rate heterogeneity across ichthyosaur phylogeny. Tree comparisons under each analytical criterion failed to select a single best tree, however, the Bayesian inference tree with gamma-distribution rate prior is

^{*}Corresponding author. Email: benjamin.moon@bristol.ac.uk

selected as the best tree based on recent analyses showing improved accuracy using this criterion. Unequivocally resolved clades include Ichthyopterygia, Ichthyosauria, Shastasauria, Euichthyosauria, Parvipelvia, and Neoichthyosauria, but with variation in their taxonomic components. Mixosauridae and Ophthalmosauridae are similarly recovered, but their definitions are modified to stem-based definitions to prevent substantial variation of included taxa. Several genera are not monophyletic: *Brachypterygius*, *Leptonectes*, *Mixosaurus*, *Ophthalmosaurus*, *Paraophthalmosaurus*, *Phalarodon*, *Platypterygius*, *Stenopterygius*, *Temnodontosaurus*, and *Undorosaurus*. Complex and variable relationships suggest the need for new characters and a re-evaluation of the state of ichthyosaur phylogenetics.

Keywords: Bayesian inference, Ichthyosauriformes, Ichthyosauria, maximum likelihood, maximum parsimony, tree selection.

Introduction

Ichthyosaurs are members of a clade of marine reptiles known from the Early Triassic through to the early Late Cretaceous (McGowan & Motani 2003). Their relative commonness, compared to other marine reptile groups, longevity, and worldwide distribution means that they are a diverse and well-known group. There are currently 114 valid species in 70 genera, with some taxa represented by several hundreds or thousands of specimens – e.g. *Ichthyosaurus* and *Stenopterygius* (Maisch & Matzke 2000) – although most are known from fewer, and less complete specimens (Cleary *et al.* 2015). Ichthyosaurs rapidly and profoundly adapted to the marine realm early in their evolution. Even the earliest known ichthyosaurs show many derived characters: paddle-like limbs; elongate, streamlined body; partial development of a tail bend and fluke; and viviparity (Motani 1999a, 2005; Motani *et al.* 2014; Chen *et al.* 2014b). Rapid diversification through the Triassic led to their occupying many niches, resulting in disparate forms (Camp 1980; Massare 1987; Sander *et al.* 2011; Motani *et*

46 *al.* 2013). Ichthyosaurs are historically important as one of the earliest recognized extinct
47 vertebrate groups (Howe *et al.* 1981; Torrens 1995).

48 Most recent work has concerned the taxonomy of ichthyosaurs: many taxa were
49 originally described over a century ago, and so are in need of revision (McGowan & Motani
50 2003; Maisch 2010). However, the interrelationships of ichthyosaurs have also been
51 investigated with the description of new species (e.g. Fischer *et al.* 2013; Roberts *et al.* 2014).
52 Increasingly, macroevolutionary trends within the group are being considered, including
53 palaeobiogeography (Bardet *et al.* 2014), diversification and extinction rates (Fischer *et al.*
54 2012; Fischer *et al.* 2016), response to extinction events (Thorne *et al.* 2011), and ecology
55 (Sander *et al.* 2011; Fröbisch *et al.* 2013; Motani *et al.* 2013; Dick & Maxwell 2015). Despite
56 this, there has been no recent attempt to include all ichthyosaur taxa in a single phylogenetic
57 analysis; this is the purpose of the present study.

58 Numerical cladistic analyses have been performed on ichthyosaurs for three decades
59 (Mazin 1981, 1982), and computational analyses for over two decades (Callaway 1989;
60 Caldwell 1996). The largest studies included most taxa only to generic level (Motani 1999c;
61 Sander 2000; Maisch & Matzke 2000; Motani *et al.* 2015), but have since had taxa and
62 characters added or modified (Thorne *et al.* 2011; Sander *et al.* 2011; Fröbisch *et al.* 2013;
63 Cuthbertson *et al.* 2013a, b). Many analyses have focused upon ichthyosaur subclades,
64 including Shastasauria (e.g. Nicholls & Manabe 2001), Mixosauridae (e.g. Jiang *et al.* 2005;
65 Jiang *et al.* 2006), Parvipelvina (e.g. Maxwell *et al.* 2012; Fischer *et al.* 2013), and Thunnosauria
66 and Ophthalmosauridae (e.g. Fernández 2007; Druckenmiller & Maxwell 2010; Fischer *et al.*
67 2012; Druckenmiller & Maxwell 2014; Fischer *et al.* 2014b; Roberts *et al.* 2014; Arkhangel'sky
68 & Zverkov 2014).

69 This study aims to (1) present an inclusive phylogenetic analysis of ichthyosaurs, for both
70 taxa and characters; (2) reappraise the definitions of the major ichthyosaur clades; and (3)
71 provide a comparison of the different methodologies and results for estimating phylogeny.

72 **Previous work**

73 Joseph and Mary Anning found the first recognized ichthyosaur materials in 1810–1811 in the
74 Lias Group at Lyme Regis, Dorset (Home 1814; Torrens 1995). Numerous ichthyosaur finds
75 were reported throughout the nineteenth century, initially from the Lower Jurassic of the
76 United Kingdom (Young 1821), but soon followed by materials collected worldwide from
77 much of the Mesozoic (Jaeger 1824; Carter 1846; Quenstedt 1852; McGowan & Motani 2003).

78 The first consideration of the internal classification of ichthyosaurs was by Kiprijanoff
79 (1881, p. 88), who separated them into two groups: Ichthyosauri Longipinnipedes and
80 Ichthyosauri Latipinnipedes, with each split into two subgroups based on tooth morphology.
81 This dichotomy was principally based upon the size and shape of the forelimb: longipinnipeds
82 have long, narrow fore and hind limbs, whereas latipinnipedes had short and wide fore and
83 hind limbs, with the hind limbs much shorter than the forelimbs, forelimb bones without
84 notches, and more phalanges than longipinnipeds. Baur (1887a, b) separated ichthyosaurs
85 into three families: Mixosauridae, Ichthyosauridae, and Ophthalmosauridae, again based on
86 forelimb morphology. Lydekker (1888) combined these two, applying Kiprijanoff's (1881)
87 classification to the Ichthyosauridae of Baur (1887a, b). Later classifications and phylogenetic
88 hypotheses extended the latipinnate-longipinnate separation to all ichthyosaurs (Merriam
89 1908; von Huene 1922, 1923a, b).

90 The first cladogram of Ichthyopterygia was included in Mazin's (1981) revision of
91 *Grippia longirostris*, featuring five characters that defined outgroups to Ichthyosauria: *Grippia*
92 was found to be the most basal ichthyopterygian, with Mixosauria and *Utatsusaurus* as

93 successive ingroups. This was then expanded to include more ichthyosaurs the following year
 94 (Mazin 1982) in a cladistic analysis with 54 taxa and 14 characters (Fig. 1A). Mazin's (1982)
 95 characters are like those used in many later analyses, although several of his characters have
 96 later been combined. The resulting cladogram did not show a latipinnate-longipinnate split,
 97 but instead a series of nested subclades, from which several families split – largely like those
 98 previously conceived. Callaway (1989) determined the relationships of shastasaurid
 99 ichthyosaurs, and used *Grippia* and *Petrolacosaurus* as outgroups, based upon his analysis of
 100 the diapsid affinities of ichthyosaurs (Mazin 1981; Callaway 1989; Massare & Callaway 1990).
 101 This was the first use of computational parsimony analysis, with 9 taxa and 33 characters.
 102 Most characters were multistate, with many being discretized ratios, but these characters
 103 have survived in many subsequent analyses and serve to mark not only Shastasauridae, but
 104 other ichthyosaur clades too.

105 A major advance in the understanding of ichthyosaur phylogeny marked the years 1999
 106 and 2000: three large, independent analyses were published that included many ichthyosaur
 107 taxa and over 100 characters each (Figs 1B–D; Motani 1999c; Sander 2000; Maisch & Matzke
 108 2000). These phylogenies yielded similar topologies, and agreed with previous cladistic
 109 analyses in having a series of nested clades marked by stepwise addition of characters (Figs
 110 1B–D). However, several families – e.g. Shastasauridae and Grippiidae – were found to be
 111 paraphyletic, leading to the concept of ichthyosaur grades (Motani 2005). Despite the
 112 different conceptions of these analyses, many of the characters were similar, but often used
 113 different coding styles: Maisch & Matzke (2000) favoured more strictly binary characters. So
 114 too did Motani (1999c), as well as tentatively using discretized ratios like Callaway (1989).
 115 Sander (2000) included several multistate characters to capture presence/absence and
 116 variation ('composite coding' of Strong & Lipscomb (1999)). In all analyses, the historical
 117 taxa of Mixosauridae (= Mixosauria *sensu* Motani [1999c]), and post-Triassic ichthyosaurs

118 (Neoichthyosauria) were recovered. Motani (1999c) and Sander (2000) also included
 119 extensive outgroups – Maisch & Matzke (2000) used only an all-zero outgroup – marking the
 120 first indication of ichthyosaurs' hupehsuchian affinities in a phylogeny, while confirming
 121 previous ideas on diapsid affinities. Criticism of all the above analyses was made in McGowan
 122 & Motani (2003).

123 Most cladistic studies following these three have tended to be extensions of Motani
 124 (1999c) or Maisch & Matzke (2000), including new taxa or character modifications.
 125 Consequently, the broad topology of ichthyosaur phylogeny has varied little since 1999. With
 126 the finding of new taxa, studies focused on subclades of Ichthyopterygia. These include
 127 Shastasauridae (Fig. 2A; Nicholls & Manabe 2001; Fröbisch *et al.* 2006; Sander *et al.* 2011),
 128 Mixosauridae (Fig. 2B; Jiang *et al.* 2005; Maisch & Matzke 2005; Jiang *et al.* 2006; Chen &
 129 Cheng 2010), and Parvipelvia and Thunnosauria (Figs 2C–E; Fernández 2007; Druckenmiller
 130 & Maxwell 2010; Fischer *et al.* 2012; Fischer *et al.* 2013). The analysis by Fröbisch *et al.*
 131 (2013) was the first to Bayesian inference rather than parsimony (Fig. 1E). Many of these
 132 studies have found genera to be non-monophyletic, and relationships to be unstable and
 133 prone to collapse. The recent discovery and description of Chinese Early and Middle Triassic
 134 fossils has added several taxa towards the base of Ichthyosauriformes, increased our
 135 knowledge of other poorly known taxa, and helped resolve the relations of ichthyosaurs to
 136 other reptile groups (Benton *et al.* 2013; Chen *et al.* 2014a; Ji *et al.* 2016). New specimens of
 137 hupehsuchians, and a general diapsid phylogenetic analysis, have lent support to an
 138 Ichthyopterygia-Hupehsuchia sister relationship, but the position of Ichthyosauromorpha
 139 within Diapsida remains uncertain (Chen *et al.* 2014a).

140 In summary, the most recent work on ichthyosaur phylogeny has resolved the group as a
 141 single clade, with a sister relationship to Hupehsuchia. The internal topology has mostly been
 142 constructed using parsimony methods as series of nested ingroups, but several large clades –

143 particularly Mixosauridae, Parvipelvia, and Neoichthyosauria – are commonly recovered and
 144 well supported. Individual taxa are, however, prone to change position depending on taxon
 145 and character sampling. These inconsistencies and lack of investigation of alternative
 146 methodologies are the impetus behind the present study.

147 **Materials and methods**

148 The compilation of the matrix and subsequent analysis follows previous studies in its
 149 methodology, but with substantial extensions to improve understanding of the tree.
 150 Specifically, a modified ‘supermatrix methodology’ was used to compile the data, and then
 151 maximum parsimony, maximum likelihood, and Bayesian inference methods were used for
 152 analysis. De Queiroz & Gatesy (2007) describe this method: concatenate separate
 153 phylogenetic matrices, which are then analysed as a single dataset. This is modified here to
 154 include the critical analysis of the characters from the input phylogenetic datasets; they are
 155 not simple concatenated. The aim of this is to exclude repeated, uninformative, and
 156 misleading characters, and to modify the characters to bring them into line with the most
 157 recent coding styles.

158 **Taxon selection**

159 Almost all valid ichthyosaur species were included: 115 operational taxonomic units (OTUs) –
 160 114 Ichthyosauriformes plus an outgroup taxon (see Online Supplemental Material Document
 161 S1.1). *Cetarthrosaurus walkeri* Seeley, 1873 was excluded as the only known material – two
 162 propodials from the Cretaceous of the UK – cannot be assigned to the fore or hind limb so
 163 cannot be reliably coded (Fischer *et al.* 2014c). While most taxa have good coverage in the
 164 literature, for some taxa – e.g. *Mixosaurus kuhnschnyderi* – specific details were not present in
 165 the publications. Twenty-five taxa (22%) have been personally observed; 13 of which (11%)

166 include the holotype (see Online Supplemental Material Document S1.2). For the ingroup, taxa
167 considered valid up to September 2017, both in previous studies and from literature review,
168 were included; the most recently named included taxon is *Ichthyosaurus somersetensis* Lomax
169 & Massare, 2017. Taxa that could be removed safely *a priori* were identified using the
170 Concatabominations method of Siu-Ting *et al.* (2015), an extension of Wilkinson's (1995) Safe
171 Taxon Removal (STR).

172 *Hupehsuchus nanchangensis* was selected as the outgroup, based upon previous analyses,
173 which have consistently found this taxon to be the immediate sister taxon to
174 Ichthyopterygia/Ichthyosauriformes (Motani 1999c; Chen *et al.* 2014b). This taxon represents
175 the best-known hupehsuchian: *Nanchangosaurus* and *Parahupehsuchus* are known only from
176 specimens where phylogenetically important parts of the body are missing or less well
177 known, particularly the skull (Chen *et al.* 2014a, b). Most of the methods used allow only a
178 single outgroup to be explicitly selected, otherwise relying on the similarities of these
179 outgroup taxa to maintain close relationships.

180 **Character list & coding**

181 The character list was assembled by critically comparing the characters used in previous
182 analyses. First, the characters of Motani (1999c) were compared with Maisch & Matzke
183 (2000), which incorporated many similar characters; Maisch & Matzke (2000, p. 8) noted this
184 similarity despite the separate genesis of the two analyses. Characters were selected based
185 upon their informativeness in the analyses from which they were derived, and their relevance
186 to ichthyosauriform ingroup relationships: characters relating specifically to a diapsid
187 outgroup were excluded. Next, additional characters from Sander (2000) were added. These
188 three large analyses incorporated most relevant characters from previous phylogenetic
189 studies on ichthyosaurs, so it was necessary to review previously suggested characters only

190 briefly. Characters from subsequent analyses were incorporated, in the same manner, up to
191 the most recent available (Roberts *et al.* 2014; Motani *et al.* 2015). In some cases, characters
192 had been modified for certain subclades. In these cases, the characters were either reverted to
193 the original form, or compared to the other clades and additional states or modifications
194 added as necessary. All characters were treated as unweighted, and most characters were
195 unordered unless they were ordered in the source analyses (see Online Supplemental
196 Material Document S1.3).

197 In evaluating each character, the following were considered: (1) similarity to other
198 characters; (2) uniqueness of character states; (3) informativeness of the character. While
199 most characters were incorporated unchanged, some were modified to meet these criteria. In
200 particular, characters were modified in accordance to their uniqueness of states using
201 reductive coding, following the suggestions of Strong & Lipscomb (1999) and Brazeau (2011).
202 Spurious groupings created by the algorithms used in maximum parsimony were
203 circumvented by collapsing zero-length branches, the default in TNT (Brazeau 2011). Some
204 characters were originally formulated to incorporate ecological differences, or their
205 morphological correlates, into phylogenetic analyses, particularly several within the study of
206 Sander (2000). These characters have been explicitly excluded in the present study. Where
207 ecologically-informative morphological characters are retained is if these do show putative
208 phylogenetic relationships – e.g. the length of the postorbital skull, abbreviated lower jaw, loss
209 of teeth. Further characters received minor modifications in polarity, as state 0 was preferred
210 for the non-ichthyosauriform outgroup. Besides designating an outgroup, most characters
211 were treated as unordered in the analyses, so this is purely an aesthetic change. The matrix
212 was assembled into NEXUS format with Mesquite version 3.2(801) (Maddison & Maddison
213 2016).

214 As many new species and characters were being incorporated into the data matrix, this
 215 was largely completed anew from the literature, with reference to previous datasets. Where
 216 characters had not been previously coded for taxa, these were added from personal
 217 observation and the literature (see Online Supplemental Material Document S1.2). This is the
 218 first complete, species-level phylogeny of Ichthyosauriformes; many taxa are being coded, or
 219 at least separated, for the first time. Taxa in need of revision were preferentially coded from
 220 the type material, but for all taxa, this was not exclusively the case.

221 **Phylogenetic analyses**

222 Two analytical criteria were used: parsimony and likelihood, under three inference methods.
 223 These criteria, and several analyses, were used to compare the results, tree selection, and
 224 support from a palaeontological dataset, a novel approach in palaeontological phylogenetic
 225 analyses. For each analysis, the commands used are included in the Online Supplemental
 226 Material Document S1.4.

227 **Maximum parsimony analyses.** Parsimony analysis was performed using TNT version 1.5
 228 (Goloboff *et al.* 2008; Goloboff & Catalano 2016) with the new technology tree fusing, ratchet,
 229 and sectorial searching algorithms of Nixon (1999) and Goloboff (1999). This was followed by
 230 tree bisection-reconnection (TBR) branch swapping to find all most parsimonious trees
 231 (MPTs) up to a maximum of 100,000 held. These settings allow for rapid analysis, while still
 232 covering many tree topologies, minimising entrapment within local minima, and all within a
 233 reasonable timeframe. An *a posteriori* analysis of ‘wildcard taxa’ used the iterative position
 234 congruence (reduced) (PCR) method of Pol & Escapa (2009). This method, and the TNT script
 235 provided by Pol & Escapa (2009), identifies taxa that cause the collapse of clades into
 236 polytomies, lists the characters that cause this instability, and suggests additional data that
 237 may solve the relationships. Instability of taxa was illustrated using a 25% cluster network of

all MPTs in Dendroscope version 3.5.7 (Huson & Scornawacca 2012) and a mean 25% consensus network of all MPTs in SplitsTree version 4.14.2 (Huson & Bryant 2006). Bremer (single decay) support values were calculated in TNT by TBR swapping on the MPTs, as were symmetrical resampling frequencies (Goloboff *et al.* 2003) using 10,000 replicates, holding one tree each time, with change probability of 33%.

Maximum likelihood analyses. Maximum likelihood analysis was carried out using RAxML AVX version 8.1.21 (Online Supplemental Material Document S1.4; Stamatakis 2014) to find the most likely tree (MLT). This used the multistate gamma-distribution mode of rate substitution within the Mkv model (Lewis 2001). RAxML is unable to accept polymorphic data, so these were replaced with uncertainties, which is how polymorphism is treated in TNT. All characters were treated as unordered. The analysis was run 2000 times, to produce a MLT with clade bootstrap values, then log likelihood (SH-tests; Shimodaira & Hasegawa 1999) were computed between this the MLT and the other trees produced.

Bayesian inference likelihood analysis. Two Bayesian-inference analyses used the Mkv model each with equal and gamma distribution priors for site rate variation respectively as implemented in MrBayes version 3.2.6 (Online Supplemental Material Document S1.4; Lewis 2001; Ronquist *et al.* 2012). Character states were unweighted and unordered, and state frequencies were defined using a symmetrical Dirichlet hyperprior fixed at infinity; this latter setting makes all state transitions equally likely. Site substitution could occur at different rates, but was time-reversible. The analyses were run for 10^8 generations with four runs of four chains that were sampled every 1000 generations, discarding the first 25%. A stop value of 0.007 was included; this was chosen as a value somewhat less than the typical convergence level of 0.01 for recovery of most supported clades. Taxon instability was shown using 25% cluster and mean consensus networks as for maximum parsimony above.

262 **Tree selection.** A combination of tests was used to select trees. All resultant trees were
 263 compared under maximum parsimony using Templeton tests in PAUP* version 4.0a150
 264 (Swofford 1998). Under maximum likelihood, the tree likelihoods were estimated in RAxML,
 265 and then CONSEL was used to compare trees using approximate unbiased tests (Shimodaira &
 266 Hasegawa 2001; Stamatakis 2014). In CONSEL, a random sample of up to 2000 trees from
 267 each of the maximum parsimony, maximum likelihood, and gamma-distributed Bayesian
 268 posterior distribution (selected using marginal likelihoods, see below) was used due to
 269 excessive computational requirements. The MLT, MPTs, and both Bayesian trees were
 270 compared with marginal likelihoods under Bayesian inference using a stepping-stone analysis
 271 in MrBayes (Fan *et al.* 2011; Xie *et al.* 2011). This used 30 steps, sampling every 1000
 272 generations for 3.1×10^7 generations, with $\alpha = 0.4$. Computational requirements meant that
 273 not all MPTs or MLTs could be tested individually, so the strict consensus-MPT and single
 274 MLT were used to constrain two stepping-stone analyses. With these tests, we attempted to
 275 reject the consensus trees under alternative inference criteria. The recent work of Wright &
 276 Hillis (2014) and O'Reilly *et al.* (2016) has shown that Bayesian inference with a gamma
 277 distribution prior produces the more accurate trees in analyses of morphological data; we
 278 therefore use this criterion as the null hypothesis against which to test. Similarity of the best
 279 trees was compared using pairwise Robinson-Foulds metrics calculated in PAUP* (Robinson
 280 & Foulds 1981).

281 **Character optimization**

282 Synapomorphies of the MPTs were optimized in TNT for unambiguous character changes
 283 across the strict consensus tree (listed under parsimony in Systematic Palaeontology below).
 284 Ancestral states for each node of the MLT were optimized under maximum likelihood in
 285 RAxML using the Mkv model (listed under likelihood in Systematic Palaeontology below).

286 Ancestral states each node, were compared to sister nodes to identify synapomorphies for
 287 named clades. Where ancestral states are uncertain due to incompleteness, these are
 288 identified as ambiguous. See also Online Supplemental Material Document S1.6.

289 **Results**

290 Concatabomination analysis identified five problematic taxa that could be removed:
 291 *Cymbospondylus piscosus*, *Isfjordosaurus minor*, *Dearcmhara shawcrossi*, and *Pervushovisaurus*
 292 *bannovkensis* (Fig. 3). With the removal of these taxa, no other redundant similarities between
 293 taxa were identified. Taxa that were coded but excluded due to poor knowledge,
 294 incompleteness, or taxonomic uncertainty include:

- 295 • *Himalayasaurus tibetensis* Young & Dong, 1972: known only from isolated jaw, teeth, and
 296 limb material (Motani & Manabe 1999).
- 297 • *Maiaspondylus lindoei* Maxwell & Caldwell, 2006: material is only known for this taxon
 298 from juveniles (Maxwell & Caldwell 2003, 2006). Ontogenetic changes in morphology are
 299 known to occur in ichthyosaurs, and may affect the coding (McGowan 1973; Motani &
 300 You 1998; Dick *et al.* 2016), although potentially only to a limited degree in the few
 301 identifiable *in utero* remains of Cretaceous ichthyosaurs (Kear & Zammit 2014). Here
 302 *M. lindoei* is conservatively excluded due to its juvenile nature and incompleteness.
- 303 • *Malawania anachronus* Fischer *et al.*, 2013: this taxon was considered equally removable
 304 to *Temnodontosaurus eurycephalus* after Concatabominations, but is less complete,
 305 missing potentially important cranial features, and is preferentially removed.
- 306 • *Pervushovisaurus bannovkensis* Arkhangelsky, 1998: this taxon is considered equally
 307 problematic to *Grendelius zhuravlevi* after Concatabominations, but is less complete and

so preferentially removed, despite removing all species within *Pervushovisaurus*; the phylogenetic position of this genus is uncertain in this study.

- *Thaisaurus chonglakmanii* Mazin *et al.*, 1991: is poorly known and only described briefly and the material is not completely prepared. McGowan & Motani (2003, p. 63) suggested that this may represent a specimen of *Chaohusaurus* and that the original description included discrepancies to the material itself.
- *Tholodus schmidi* Meyer, 1849: poorly known and described, and is taxonomically ambiguous, having been allied to Omphalosauridae, which is excluded here following Motani (2000).

The analyses reported below were carried out after removal of these taxa: 104 OTUs – ingroup taxa and one outgroup.

All analyses recover the familiar stepwise backbone relationships found in previous analyses in their resulting best trees (Figs 4, 6, 7; Online Supplemental Material figures S1, S2, S3). Successive ingroup clades are mostly ‘ladderized’, representing stepwise evolution where each clade is marked by a gradual acquisition of characters from its sister clade. Several genera are found to be monophyletic throughout all or most analyses, such as *Toretocnemus*, *Cymbospondylus* – excluding the problematic *C. piscosus* – and *Shastasaurus*, even when member species were largely incomplete. Monophyletic Mixosauridae and Shastasauria, complete as previously found, or parts thereof, are also recovered. However, several clades repeatedly form unresolved polytomies in consensus – particularly the most basal ichthyosaurs and Ophthalmosauridae. Removing the least stable taxa improves the resolution of the basal ichthyosaurs and Ophthalmosauridae somewhat.

The term ‘core’ is used below to mean the monophyletic clade including most species within a genus, and specifically the type species of a genus. Unnamed clades are referred to

332 with a '+' – i.e. *Ophthalmosaurus icenicus* + *Platypterygius hercynicus*, indicating the minimally
 333 inclusive clade including the named taxa.

334 **Parsimony analysis**

335 Parsimony analysis found 11,536 MPTs each with length 1666 steps. The strict consensus is
 336 poorly resolved, with four large polytomies (Fig. 4): one basally (the clade comprising
 337 *Parvinatator wapitiensis* + *Ichthyosaurus communis*), one at the base of Hueneosauria
 338 (*Mixosaurus cornalianus* + *Ichthyosaurus communis*), one at the base of Neoichthyosauria
 339 (*Temnodontosaurus platyodon* + *Ichthyosaurus communis*), and Ophthalmosauridae
 340 (*Ophthalmosaurus icenicus* + *Platypterygius hercynicus*). However, many basal
 341 Euichthyosauria and clades within Neoichthyosauria are resolved. Resolution is substantially
 342 increased in the 50% majority rule tree (Online Supplemental Material Figure S1). The
 343 consistency (CI) and retention indices (RI) for both strict consensus and 50% majority rule
 344 trees are low: CI = 0.150 and 0.175; RI = 0.521 and 0.601 respectively; rescaled consistency
 345 indices (RCI) = 0.0782 and 0.105 respectively; homoplasy is rife. All resolved clades have a
 346 Bremer support value ≥ 1 ; many clades have support ≥ 2 ; Neoichthyosauria, Leptonectidae,
 347 Stenopterygiidae (*sensu* Maisch 1998), and Ophthalmosauridae, among others, have support
 348 ≥ 3 . Resampling values were, however, low: few clades have support $\geq 50\%$; the highest
 349 support was found for core *Toretocnemus* (79%), *Suevoleviathan* (69%), core
 350 *Temnodontosaurus* (89%). Regions of instability are shown in cluster and consensus networks
 351 largely around the base of Hueneosauria and Ophthalmosauridae (Fig. 5; Holland & Moulton
 352 2003; Huson & Bryant 2006; Huson & Scornawacca 2012).

353 PCR pruning identified 31 OTUs and two nodes to remove (Table. 1). Analysis using the
 354 script of Pol & Escapa (2009) did not complete due to the number of taxa pruned; using the
 355 version built into TNT removed the taxa listed in Table 1. These represent some of the least

known of the included taxa, but these may still be coded for many characters (i.e. *Ichthyosaurus conybeari*). The resultant pruned tree has slightly greater resolution in basal Neoichthyosauria and Ophthalmosauridae (Online Supplemental Material Figure S2). The CI, RI, and RCI values are also increased by removing OTUs (not nodes) to 0.223, 0.706, and 0.157 in strict consensus and 0.233, 0.721, and 0.168 for the 50% majority rule consensus respectively.

Maximum likelihood analysis

The MLT found using RAxML is qualitatively like to the majority rule consensus of MPTs (Fig. 6). The basal taxa are paraphyletic with respect to Ichthyosauria, and the overall topology comprises a series of nested ingroups. Bootstrap supports are generally low, particularly for the backbone of the tree. Several small clades do receive values > 50%: *Toretocnemus* (93%), core *Temnodontosaurus* (75%), *Shastasaurus* (62%), and *Suevoleviathan* (61%). Eight bootstrap recovered trees were found to be significantly worse than the MLT (5%) using SH-tests (also eight trees at 2% and 1%; Online Supplemental Document S1.5). Despite Mixosauridae being recovered, this clade is not strongly supported (57% bootstrap), nor are other major clades such as Hueneosauria (31%) and Merriamosauria (8%).

Bayesian-inference likelihood analysis

Analyses in MrBayes converged in both cases, but the resultant 50% majority rule consensus trees are poorly resolved, although the equal-distribution rates prior tree has greater resolution than the gamma-distribution rates prior tree (Fig. 7; Online Supplemental Material Figure S3). The posterior distributions in all cases overlap, but are different to the prior distributions (Online Supplemental Material Figure S4). The gamma-distribution rates prior is strongly supported over the equal-distribution rates prior (Bayes factor differences,

379 $\delta B = 267.52$; Online Supplemental Material Document S1.5; Kass & Raftery 1995), so
 380 discussion below will focus on that analysis. The consensus tree comprises a series of
 381 polytomies: the largest found at the base of Hueneosauria, Merriamosauria, Neoichthyosauria,
 382 and Ophthalmosauridae – comprising approximately the Middle–Late Triassic, Early Jurassic,
 383 and post-Early Jurassic taxa respectively (Fig. 8). Clade credibility values, where resolved, are
 384 often high – e.g. *Toretocnemus* (99% and 96% for equal- and gamma-distribution rate priors
 385 respectively), *Shastasaurus* (90% and 99%), Neoichthyosauria (73% and 98%), and
 386 Ophthalmosauridae (95% and 97%).

387 **Tree selection**

388 Templeton tests found the MPTs to be equally the best; all other trees were significantly
 389 worse ($p \leq 0.05$; Online Supplemental Material Document S1.5, S5). Approximate unbiased
 390 tests found the MLT to be the best; 1859 trees were significantly different from this tree
 391 ($p \leq 0.05$; Online Supplemental Material Document S1.5, S5). Of the non-significantly different
 392 trees, 327 were MPTs, 341 from the gamma distribution rates prior Bayesian inference
 393 posterior distribution, and 1191 from the ML bootstrap search. Under Bayesian inference, the
 394 consensus-MPT and MLT were significantly worse than the Bayesian inference tree
 395 ($\delta B > 2000$; Online Supplemental Material Document S1.5, S5). The strict consensus-MPT and
 396 MLT were the most different (Robinson-Foulds metric, RF = 97), whereas the consensus-MPT
 397 (RF = 37) was more like the consensus gamma-distribution rate prior Bayesian inference tree
 398 than the MLT (RF = 84) was. Following O'Reilly *et al.* (2016), the Bayesian inference tree with
 399 gamma-distribution rate prior is selected as the best tree (Fig. 7; Online Supplemental
 400 Material Document S5). However, additional unresolved relationships are inferred based on
 401 consensus in the other trees found.

402 **Systematic palaeontology**

403 The following taxonomy is based upon the preferred phylogeny (Fig. 7). Unambiguous
 404 synapomorphies optimised in TNT (parsimony) and in RAxML (likelihood) are shown where
 405 the clade is resolved for the MPTs, MLT, and preferred tree (see Online Supplemental Material
 406 Document S1.6 and S1.7).

407 Clade **Ichthyosauromorpha** Motani *et al.*, 2015

408 **Definition.** The last common ancestor of *Hupehsuchus nanchangensis* and *Ichthyosaurus*
 409 *communis*, and all of its descendants [node-based] (Motani *et al.* 2015).

410 **Discussion.** Motani (1999c) suggested the name Ichthyosauromorpha for the stem-based
 411 equivalent definition of his Ichthyopterygia as the maximally inclusive clade of ichthyosaurs,
 412 but refrained from a formal proposition, as the sister group was then uncertain. Recent
 413 discovery and re-description of several hupehsuchians has shown that this group is
 414 consistently found as the sister to ichthyosaurs (Chen *et al.* 2014a, b). Motani *et al.* (2015)
 415 found *Cartorhynchus* and *Chaohusaurus* to be the most basal ichthyosaur taxa. They erected
 416 Ichthyosauromorpha and Ichthyosauriformes for the node that includes *Hupehsuchus*
 417 *nanchangensis* + *Ichthyosaurus communis*, and the stem that includes *Ichthyosaurus communis*
 418 but not *Hupehsuchus nanchangensis* respectively.

419 Clade **Ichthyosauriformes** Motani *et al.*, 2015

420 **Definition.** The most inclusive clade that includes *Ichthyosaurus communis*, but not
 421 *Hupehsuchus nanchangensis* [stem-based] (Motani *et al.* 2015).

422 **Discussion.** Motani *et al.* (2015) found *Cartorhynchus* and *Chaohusaurus* to be the most basal
 423 ichthyosauriform taxa, and indicated in their fig. 4 that Ichthyopterygia was at the node that

424 includes *Chaohusaurus* and all other ichthyosaurs, but no definitions were formally emended.
 425 Here, the most recent definitions of Motani (1999c) are used in assigning names to these
 426 clades.

427 Clade **Ichthyopterygia** Owen, 1859

428 **Definition.** The last common ancestor of *Ichthyosaurus communis*, *Utatsusaurus hataii*, and
 429 *Parvinatator wapitiensis*, and all its descendants [node-based] (Motani 1999c).

430 **Discussion.** Ichthyopterygia was erected by Owen (1859, p. 159) as an order within Reptilia
 431 to hold the known ichthyosaur taxa – then limited to the genus *Ichthyosaurus*. Wiman (1929,
 432 1933) later suggested that *Grippia longirostris* should be positioned alongside Ichthyosauria
 433 within Ichthyopterygia. *Parvinatator wapitiensis* is consistently found to be more basal than
 434 *U. hataii*, which places Ichthyosauria within this Ichthyopterygia as was found previously by
 435 Motani (1999c) (see discussion of Ichthyosauria below).

436 Grippioidea is recovered only in the MLT, and basal Ichthyopterygia are poorly resolved.
 437 The lack of the most basal Ichthyosauriformes – e.g. *Cartorhynchus* and *Sclerocormus* – in the
 438 study of Ji *et al.* (2016) makes it difficult to compare the character trends to this study.
 439 However, in the preferred tree here, the change from a dorsally to laterally located external
 440 naris occurs around the Ichthyopterygia–Hueneosauria transition; the presence of a manual
 441 pisiform in this study comes with Ichthyopterygia also. Multiple maxillary rows are found in
 442 the most basal Ichthyosauriformes, but lost early in Ichthyosauria, so that it is not present in
 443 Hueneosauria (Maisch & Matzke 2000; Ji *et al.* 2016). Ichthyopterygia possess enlargement of
 444 the supratemporal, but is reduced in basal Hueneosauria. The definition of ‘moderate
 445 enlargement’ used here reflects the changing cases in basal Ichthyopterygia versus more
 446 derived taxa; more extensive enlargement occurs in Neoichthyosauria. A modified definition

447 for this character could define Eoichthyosauria or Hueneosauria more clearly by including
 448 contacts with the supratemporal, although these are incorporated into other characters.

449 Clade **Eoichthyosauria** Motani, 1999b

450 **Definition.** The last common ancestor of *Grippia longirostris* and *Ichthyosaurus communis*,
 451 and all its descendants [node-based] (Motani 1999c).

452 **Discussion.** This clade is not resolved typically due to a polytomy at the base of
 453 Ichthyopterygia. Under the original definition, *Chaohusaurus* was included as the sister to
 454 *Grippia* in Grippidia (Motani 1999c). Eoichthyosauria is recovered in the majority rule
 455 consensus-MPT as including Ichthyosauria and Ichthyopterygia within as *Grippia longirostris*
 456 is recovered more basal than *Utatusaurus hataii*. (See also Ichthyopterygia above.)

457 Clade **Ichthyosauria** de Blainville, 1835

458 **Definition.** All taxa more closely related to *Ichthyosaurus communis* than to *Grippia*
 459 *longirostris* [stem-based] (Motani 1999c).

460 **Discussion.** Class Ichthyosauria was erected by de Blainville (1835) to include *Ichthyosaurus*,
 461 which was the only named genus at that time. Later, Owen (1859) placed ichthyosaurs in
 462 Order Ichthyopterygia, within Class Reptilia. Again, *Ichthyosaurus* was then the only included
 463 genus, but this included specimens that would later be split into the genera *Leptonectes*,
 464 *Mixosaurus*, *Stenopterygius*, and *Temnodontosaurus*. Wiman (1929) originally included *Grippia*
 465 in an order separate from Ichthyosauria, but later suggested that both these should be
 466 included as suborders within Order Ichthyopterygia (Wiman 1933). Mazin (1982) followed
 467 this, in portraying Ichthyopterygia to include all ichthyosaurs *sensu lato*, with an ingroup
 468 clade Ichthyosauria that excluded his Mixosauridae, *Grippia longirostris*, *Phalarodon fraasi*,

469 and *Omphalosaurus*. In revising this, Motani (1999c) redefined Ichthyopterygia based on his
 470 reversed topology of *Grippia* and *Utatsusaurus*: following Mazin's (1982) definitions on
 471 Motani's (1999c) topology would place Ichthyopterygia as a clade within Ichthyosauria,
 472 respecting the relative position from their Linnaean origins (order- vs. class-level
 473 respectively). With *Utatsusaurus* being recovered basally here, the relative positions of
 474 Ichthyosauria and Ichthyopterygia are retained from Wiman (1933) and Motani (1999c),
 475 except in the majority rule consensus-MPT in which these clade positions are reversed.

476 Clade **Hueneosauria** Maisch & Matzke, 2000

477 **Definition.** The last common ancestor of *Mixosaurus cornalianus* and *Ophthalmosaurus*
 478 *icenicus*, and all its descendants [node-based] (Maisch & Matzke 2000).

479 **Synapomorphies. Parsimony.** prefrontal-postfrontal contact absent [37:1→0]; anterior
 480 terrace of the temporal fenestra present [74:0→1].

481

482 **Discussion.** Hueneosauria is recovered within Ichthyosauria, but containing some that have
 483 been considered more basal (Fig. 7; *Parvinatator wapitiensis* and *Pessopteryx nisseri*).
 484 *Cymbospondylus* is found within Hueneosauria in all analyses (Sander 2000; Maisch & Matzke
 485 2000), but was recovered more basal to Hueneosauria by Motani (1999c) and Ji *et al.* (2016).
 486 The support for this clade moderate to high (80% in the preferred tree; Fig. 7), and subclades
 487 within Hueneosauria are better defined and supported. Similarly, which taxa are also within
 488 the subclade Merriamosauria is variable. An important resolution is the presence of the
 489 postparietal in *Cymbospondylus* and *Phantomosaurus*: is it present in both taxa? Is this a single
 490 medial ossification or paired lateral ossifications? does the same condition occur in both taxa?
 491 The previous interpretations of these taxa disagree with each other (Maisch & Matzke 2004;

492 Fröbisch *et al.* 2006; Maisch & Matzke 2006) leading too uncertainty: should *Phantomosaurus*
 493 form a clade with *Cymbospondylus* united by this feature? or are separate conditions
 494 represented?

495 Contact between the prefrontal and postfrontal is not present in many of the most basal
 496 taxa, but has been reported in *Chaohusaurus chaoxianensis* and *Sclerocormus parviceps* (Jiang
 497 *et al.* 2016; Zhou *et al.* 2017). It is not present in the most basal Ichthyopterygia, but almost all
 498 known Hueneosauria do possess this state. Short caudal centra are a feature of all adequately
 499 known Hueneosauria, but is also found in *Sclerocormus parviceps* (Jiang *et al.* 2016). The
 500 definition of ‘short’ is vague, and this interpretation could be open to change, in which case
 501 this will be a feature of Hueneosauria alone. Additionally, the chosen definition ‘short’ must
 502 take in the variable size of ichthyosaur caudal vertebrae. Many Neoichthyosauria have
 503 vertebral centrum height/length ratios (i.e. apparent ‘shortness’) of 2–4 (Buchholtz 2001;
 504 Fischer *et al.* 2011), but this becomes less posteriorly. Similar data for Triassic ichthyosaurs is
 505 less frequent, so it’s difficult to be certain whether they reach a similar ratio, or that ratio is
 506 noticeably less and centra relatively longer. Hueneosauria are also united by a regularly
 507 rounded anterior orbital margin, although in some more derived taxa this is modified into an
 508 angled margin – e.g. *Cryopterygius kristiansenae* (Druckenmiller *et al.* 2012). It also in basal
 509 Hueneosauria that the coronoid becomes non-ossified. At the base of Hueneosauria, the
 510 number of presacral vertebrae is optimized to be >55. This is due to the non-Mixosauridae
 511 that have elongated trunk regions – e.g. *Cymbospondylus* and *Shastasaurus* – and is reduced in
 512 Euichthyosauria. An alternative interpretation of this character could be that presacral
 513 vertebral count is increased only in the *Cymbospondylus* + *Shastasaurus* clade, not including
 514 the basal Hueneosauria; there would still be a reversal in more derived Merriamosauria,
 515 however.

Clade **Mixosauridae** Baur, 1887a

Emended definition. All taxa more closely related to *Mixosaurus cornalianus* than to *Ichthyosaurus communis* [stem-based].

Synapomorphies. Likelihood. Maxilla meets prefrontal [14:0→1]; external naris elongate [26:0→1]; postparietals absent [52:1→0]; parietal foramen well anterior to supratemporal fenestra [54:0→1]; postfrontal-supratemporal contact present [57:0→1]; large anterior terrace of the temporal fenestra [75:0→1]; interpterygoid vacuity absent [86:1→0]; basioccipital without notochordal pit [95:1→0]; posterior tooth crown rounded [149:0→1]; interclavicle triangular [181:2→1]; coracoid with anterior notch [185:1→0]; intermedium with one facet larger than the other(s) [235:0→1].

Discussion. Motani's (1999c) original definition of Mixosauria used *Mixosaurus cornalianus* and *M. nordenskioeldii*. The latter of these taxa is now considered a *nomen dubium* (Schmitz 2005). The definition of this clade was emended by Ji *et al.* (2016) as the *M. cornalianus* + *Phalarodon fraasi* node, however, in the present phylogeny that demarcates only those two taxa (Fig. 7); a stem-based definition that includes all similar taxa is preferred. Mixosauridae are known from good specimens, with well-defined apomorphies, but their internal taxonomy needs revision. This redefinition aims to provide stability to the clade.

That Mixosauridae is not resolved under parsimony is surprising considering the number of potential apomorphies present in these taxa. Support for Mixosauridae in the preferred tree is strong (98%), a relatively high support is found under maximum likelihood too (57%), and most trees support the resolution of Mixosauridae in the majority rule consensus-MPT (85%). There is, however, notable uncertainty in the topology of basal Hueneosauria (Fig. 5). Further characters that can be optimized support the monophyly of Mixosauridae; these are mostly

539 like those previously defined and reflect the modifications of the skull due to their unusual
 540 ecology: large anterior terrace of the temporal fenestra, supratemporal sheet over temporal
 541 fenestra, short postorbital region, rounded posterior teeth (Motani 1999b, c; Maisch & Matzke
 542 2000). The incompleteness of *Phalarodon major* and its position within Merriamosauria in the
 543 preferred tree suggests that this taxon may be the cause of Mixosauridae non-monophyly in
 544 the consensus-MPT.

545 Clade **Merriamosauria** Motani, 1999b

546 **Definition.** The last common ancestor of *Shastasaurus pacificus* and *Ichthyosaurus communis*,
 547 and all its descendants [node-based] (Motani 1999c).

548 **Discussion.** Basal Merriamosauria form a polytomy (Fig. 7). Many of the unresolved
 549 merriamosaurian taxa here have been previously resolved in Euichthyosauria (Motani 1999c;
 550 Maisch & Matzke 2000). Where recovered, the support for Merriamosauria is low. The poor
 551 resolution of this clade means that taxa otherwise described as ‘shastasaur-grade’ are not
 552 certainly with Shastasauria or Euichthyosauria.

553 Loss of the postparietal occurs in some optimizations of this clade as *Phantomosaurus*
 554 *neubigi* and *Cymbospondylus* and near sister taxa to Merriamosauria; however, this character
 555 is problematic due to interpretation of the cranium of *Cymbospondylus* (Maisch & Matzke
 556 2004; Fröbisch *et al.* 2006), and is a reversal to the same state as more basal non-
 557 Hueneosauria. Equally, several characters associated with the skull and dentition may be
 558 spread across basal Hueneosauria due to the derived positions of *Phalarodon major* and
 559 *Wimanius odontopalatus*, which have otherwise been considered more basal (Motani 1999c).
 560 Reduction of the maxilla occurs in Merriamosauria, and is coded to some degree in
 561 Neoichthyosauria + *Callawayia neoscapularis*, *Shastasaurus*, and *Shonisaurus*, as was coded by

562 Sander (2000). However, the degree of reduction in the maxilla is variable, despite the maxilla
 563 being reduced compared to more basal Hueneosauria. Differences of interpretation may occur
 564 based on the lateral coverage of the maxilla by the premaxilla anteriorly and the lachrymal
 565 and jugal posteriorly. Additionally, the loss of teeth in Shastasauria was accounted for by
 566 Sander (2000) and Maisch & Matzke (2000). Contribution of the frontal to the supratemporal
 567 fenestra is present in basal Hueneosauria, but also found in more derived
 568 Ophthalmosauridae – e.g. *Platypterygius australis* (Kear 2005) – it is not present in basal
 569 Merriamosauria and Neoichthyosauria (Ji *et al.* 2016). However, the ventral extent of the
 570 frontal can be much greater posteriorly than dorsally; should this character incorporate the
 571 total dorsal and ventral contribution of the frontal, it would overlap more with character 41
 572 (Fischer *et al.* 2011), but potentially also exclude the reversal of this character.

573 Clade **Shastasauria** Motani, 1999b

574 **Definition.** All taxa more closely related to *Shastasaurus pacificus* than to *Ichthyosaurus*
 575 *communis* [stem-based] (Motani 1999b).

576 **Synapomorphies. Likelihood.** Maxilla hidden laterally by jugal [13:0→1]; nasal-postfrontal
 577 with extensive contact [22:0→1]; frontals flat to concave in dorsal view [39:0→1]; postorbital
 578 triradiate [58:1→0]; squamosal without posterior descending process [71:1→0]; pterygoid
 579 with posteromedial process [90:1→0]; surangular without dorsal process [119:1→0]; teeth
 580 absent [128:0→1]; anterior dorsal centra rib facets not confluent with anterior margin
 581 [162:0→1]; scapula with blade shaft [196:0→1]; ulna proximally narrower than distally
 582 [224:1→0]; ilium plate-like [254:1→0]; femur ventral process same size as dorsal process
 583 [268:0→1]; femur with anterodistal facet [270:0→1]; tibia wider than long [272:0→1].

584 **Discussion.** This clade is defined as stem-based alongside a polytomy with other taxa that are

usually considered part of this group, or closely related – ‘shastasaur-grade’, e.g. *Besanosaurus*
leptorhynchus and Euichthyosauria as in Ji *et al.*’s (2016) Shastasauridae. However, because of
 this lack of resolution, this clade, as defined, includes only *Shastasaurus*.

Numerous synapomorphies are found under maximum likelihood due to the small side of
 the clade and the similarity and monogeneric relations of the taxa included within. Additional
 characters that separate *Shastasaurus* include medium to large foramina on the lachrymal;
 slender lower jaw; and interosseous foramen between the fore limb epipodials (Maisch &
 Matzke 2000; Sander *et al.* 2011). Other features that have been attributed the ‘shastasaur-
 grade’ related to the skull and fore limb become paraphyletic character transitions through
 the non-Parvipelvia Euichthyosauria: similar limb morphologies are present in
Guizhouichthyosaurus and *Besanosaurus* (Dal Sasso & Pinna 1996; Ji *et al.* 2013).

Clade **Euichthyosauria** Motani, 1999b

Definition. All taxa more closely related to *Ichthyosaurus communis* than to *Shastasaurus*
pacificus [stem-based] (Motani 1999c).

Synapomorphies. Parsimony. Nasal reaches distinctly over orbit [17:0→1]; nasal contacts
 postfrontal [21:0→1].

Discussion. Euichthyosauria defines the branch between the two polytomies of
 Merriamosauria and Parvipelvia in the preferred phylogeny (Fig. 7), but is better resolved and
 includes numerous non-parvipelvic taxa in the consensus-MPT and MLT (Figs 4, 6). The
 possibility of a novel, although poorly supported, Euichthyosauria ‘side clade’ – *Toretocnemus*
californicus + *Californosaurus perrini* – is presented in the MLT but poorly supported (Fig. 6).

606 The posterior extent of the nasal bones in Neoichthyosauria is greater than in more basal
 607 ichthyosaurs (Motani 1999c; Maisch & Matzke 2000), yet the extent is continuous. The
 608 location ‘above the orbit’ can be arbitrarily defined, however, here it is applied generally to
 609 traditional Neoichthyosauria. More basal Euichthyosauria do present nasal bones extended
 610 dorsal to the anterior orbit margin but these do not extend so far posteriorly; there may be
 611 contact with the postfrontal posteriorly as in *C. neoscapularis* and *G. tangae* (Nicholls &
 612 Manabe 2001; Maisch *et al.* 2006; Shang *et al.* 2012; Ji *et al.* 2016). In these taxa, the nasal is
 613 not so visible in lateral view. Including these taxa would position the extensive posterior nasal
 614 as a more basal feature of Merriamosauria, or potentially include *C. petrinus* to include basal
 615 Hueneosauria (Fröbisch *et al.* 2006).

616

617 Clade **Parvipelvia** Motani, 1999b

618 **Emended definition.** The last common ancestor of *Macgowania janiceps*, *Hudsonelpidia*
 619 *brevirostris*, and *Ichthyosaurus communis*, and all of its descendants [node-based] (Motani
 620 1999c).

621 **Synapomorphies. Parsimony.** Intermedium proximally pointed [232:0→1]; ischium and
 622 pubis similarly sized [259:0→1]; ischium or ischiopubis rod-like [260:0→1].

623 **Likelihood.** Humerus with markedly concave anterior margin [199:1→2].

624 **Discussion.** Parvipelvia is resolved but not well supported (53%) in the preferred phylogeny
 625 (Fig. 7), but not separated from Neoichthyosauria or Thunnosauria. The relationships
 626 between *M. janiceps*, and more derived taxa are uncertain and there is no consensus between
 627 the resultant trees (Figs 4, 6, 7). The original definition referred only to the genus
 628 *Ichthyosaurus*, whereas here this is extended and clarified to the type species, *I. communis*.

629 Parvipelvia includes *H. brevirostris*, *M. janiceps*, and Neoichthyosauria at its greatest extent,
 630 and few characters support this clade separate to Neoichthyosauria. These most basal
 631 Parvipelvia taxa are poorly known, and most of the discussion of Neoichthyosauria is
 632 applicable to Parvipelvia also (see below). Most clearly, Parvipelvia is associated with the
 633 strong reduction of the pelvic girdle, but this is a continuation of reduction in Merriamosauria
 634 or throughout all Ichthyosauriformes, incorporating the loss of contact between the pelvis and
 635 vertebral column in Hueneosauria (Eoichthyosauria?). there is no easy definition of the size of
 636 the pelvis beyond, so states have been coded largely based on previous hypotheses of
 637 relations (Motani 1999c; Maisch & Matzke 2000; Ji *et al.* 2016). Specifically in the pelvis, the
 638 ilium becomes styloid in the clade containing *Qianichthyosaurus zhoui* + Parvipelvia; another
 639 indicator of pelvic reduction. That ichthyosaurs do not lose the hind limbs completely is
 640 interesting considering that they are lost in Cetacea; perhaps they still served some purpose
 641 in swimming? perhaps related to the lateral versus dorsoventral undulatory modes of
 642 locomotion?

643 Clade **Neoichthyosauria** Sander, 2000

644 **Emended definition.** The last common ancestor of *Temnodontosaurus platyodon* and
 645 *Ichthyosaurus communis*, and all of its descendants [node-based] (Sander 2000).

646 **Synapomorphies. Parsimony.** Ulnare smaller than intermedium [229:0→1].

647 **Discussion.** Neoichthyosauria was erected to include the monophyletic post-Triassic
 648 ichthyosaur taxa (Sander 2000). The base of this clade is a large polytomy with Parvipelvia
 649 and *Temnodontosaurus* is polyphyletic within this clade. The original definition used only the
 650 genus *Ichthyosaurus*; here it is clarified to the type species *I. communis*. Maisch & Matzke
 651 (2000) used a definition involving *T. platyodon* and *Ophthalmosaurus icenicus*, but the

652 emendation from Sander's (2000) original is preferred here. The base of this clade is
 653 confluent with Parvipelvina in the preferred phylogeny (Fig. 7) and the positions of taxa within
 654 and immediately sister to Neoichthyosauria is highly variable across the recovered trees (Figs
 655 4, 6, 7; Online Supplemental Material Figure S1). Neoichthyosauria is better resolved under
 656 equal-distribution rather than gamma-distribution rates prior Bayesian inference suggesting
 657 heterogeneity in state transitions between characters in this part of the tree.

658 Neoichthyosauria here potentially includes the development of the caudal fluke into a
 659 crescentic tail fin, although this may extend to Parvipelvina. While this is most clearly known
 660 from ichthyosaurs with soft tissue preservation, osteological correlates are present in the
 661 development of a clear tail bend. This has been preserved in many Early Jurassic taxa from the
 662 UK and Germany, including *T. trigonodon*, *L. tenuirostris*, *I. communis*, and *E. longirostris*
 663 (McGowan & Motani 2003). Diagnoses of Thunnosauria (see below) include the shortening of
 664 the tail relative to the body (Maisch & Matzke 2000), which occurs in only some taxa showing
 665 the well-developed tail bend. This suggests a two-step evolution of improved swimming
 666 efficiency within Parvipelvina: tail fluke, followed by stockier (more powerful?) tail.
 667 Neoichthyosauria share aulacodont dentition (Sander 2000; Maisch & Matzke 2000),
 668 however, poor preservation of more basal Euichthyosauria makes it uncertain whether this is
 669 limited to Neoichthyosauria or more extensive. The dorsoventral extent of the maxilla is
 670 reduced posteriorly in Neoichthyosauria (Druckenmiller & Maxwell 2010), however, this
 671 coincides with a reduction of the postnarial process of the maxilla and the anterior extent of
 672 the jugal and lachrymal to cover the maxilla. A large postnarial process of the maxilla is found
 673 prominently in Mixosauridae, but a similar structure is also present in *Platypterygius australis*
 674 (Jiang *et al.* 2005; Kear 2005; Jiang *et al.* 2006); despite the morphological similarity these do
 675 not represent homology. However, the effects of the extensive postnarial process are
 676 widespread: several other characters related to bones surrounding the external naris and

677 anterior orbit are affected by this structure, and mutually exclusive states – e.g. the
 678 premaxilla-lachrymal contact; prefrontal-external naris contact.

679 Clade **Leptonectidae** Maisch, 1998

680 **Definition.** The last common ancestor of *Eurhinosaurus longirostris* and *Leptonectes*
 681 *tenuirostris*, and all of its descendants [node-based] (Maisch 1998).

682 **Synapomorphies. Parsimony.** Frontal with widest exposure posteriorly [40:1→0];
 683 supratemporal fenestra posteriorly narrower than anterior [73:1→0]; quadratojugal located
 684 posteriorly [77:0→1]; quadratojugal mostly exposed posteriorly [78:0→1]; cheek largely
 685 oriented posteriorly [85:0→1]; radial and ulnar facets of the humerus equal size [209:0→1];
 686 manual metacarpals II & IV rounded [246:2→1]; proximal manual phalanges mostly rounded
 687 [250:2→1]; femur with smaller ventral process than dorsal [268:1→0].

688 **Likelihood.** Maxilla excluded from external naris [15:0→1]; nasal contacts postfrontal
 689 [21:0→1]; prefrontal with little exposure [35:1→2]; dentition strongly reduced [129:0→1];
 690 haemapophyses present [176:1→0]; rounded manual metacarpals II & VI [246:2→1];
 691 metacarpal V absent [247:0→1]; mostly rounded proximal manual phalanges [250:2→1];
 692 ischium and pubis not fused laterally [257:1→0]; tibia and fibula do not contact proximally
 693 [277:1→0].

694 **Discussion.**

695 *Excalibosaurus costini* is most frequently recovered as the sister taxon to *Leptonectes solei*,
 696 despite the well-documented similarities with *E. longirostris*. Leptonectidae is not recovered
 697 in the preferred tree (Fig. 7), but is found under both maximum parsimony and likelihood
 698 (Figs 4, 6). While the position of this clade within Neoichthyosauria is unresolved in the

699 consensus-MPT, it is located within Thunnosauria in the MLT; a more derived position than
 700 previously found (Ji *et al.* 2016; Fischer *et al.* 2016). Leptonectidae also shows possible
 701 morphological convergence with the evolution of several longirostrine ichthyosaurs in the
 702 Early Jurassic – e.g. *Temnodontosaurus azerguensis* and *Hauffiopteryx typicus* (Martin *et al.*
 703 2012; Marek *et al.* 2015). While *H. typicus* is typically resolved in a more derived position
 704 close to Thunnosauria, similar to Marek *et al.* (2015), the position of *T. azerguensis* is less
 705 certain and has a relatively long branch.

706 The allying of *H. typicus* with Leptonectidae (but not in the preferred tree) is mostly a
 707 result of morphological convergence associated with the shortening of the posterior skull and
 708 slender snout. *Hauffiopteryx* does not have the distinctly posterior orientation of the cheek
 709 region seen in more derived Leptonectidae, but the similar morphology of the skull has
 710 effected similar changes between this taxon and Leptonectidae. Synapomorphies of
 711 Leptonectidae + *H. typicus* include the slender premaxillary segment, which was defined here
 712 based on the condition in Leptonectidae, as this was not clearly defined by Motani (1999c);
 713 such a condition is also found in the longirostrine *Temnodontosaurus azerguensis*. While these
 714 taxa are here recovered together, these ecological convergences may be due to homoplastic
 715 characters reducing their utility.

716 Clade **Thunnosauria** Motani, 1999b

717 **Definition.** The last common ancestor of *Stenopterygius quadriscissus* and *Ichthyosaurus*
 718 *communis*, and all of its descendants [node-based] (Motani 1999c).

719 **Discussion.** Thunnosauria is not found separately from Neoichthyosauria in the preferred
 720 tree (Fig. 7) or consensus-MPT (Fig. 4) as the latter clades are not resolved basally (Figs 5, 8).
 721 Thunnosauria is recovered in the MLT, poorly supported (Fig. 6), but in a similar position

722 relative to other taxa as found by Motani (1999c) and Ji *et al.* (2016) – more derived than
 723 *Temnodontosaurus*, but more basal than *Stenopterygius*.

724 Thunnosauria was diagnosed by Ji *et al.* (2016) including an absence of the anterior
 725 flange of the humerus. This was originally coded by Motani (1999c) as ‘present, but reduced
 726 proximally’ and is coded as such for some Thunnosauria by Ji *et al.* (2016). The definition of
 727 this character is open to interpretation, and loss of the anterior flange removes an important
 728 defining feature of Triassic Ichthyosauriformes. In the interpretation used here, the anterior
 729 flange is reduced proximally in Neoichthyosauria as there is clearly no anterior projection
 730 present anterior to the main humeral shaft. However, the anterodistal process or tuberosity of
 731 the humerus is present in many basal Parvipelvia, which is treated as the distal extent of the
 732 anterior flange, as implied by Motani (1999c), and included by Ji *et al.* (2016). The tail of
 733 ichthyosaurs progressively shortens through phylogeny, however, the change from being
 734 longer to shorter than the body is uncertain; this was optimized as a synapomorphy of
 735 Thunnosauria by Maisch & Matzke (2000). The coding scheme used finds this true for most
 736 traditional Thunnosauria, excluding – e.g. *Temnodontosaurus* and *Leptonectes* – yet more basal
 737 Merriamosauria are also coded with short tails – e.g. *Qianichthyosaurus zhoui*. This appears to
 738 be some level of convergence, but the proportions of *Q. zhoui* suggests that it could be coded
 739 with a longer tail

740 Clade **Baracromia** Fischer *et al.*, 2013

741 **Definition.** The last common ancestor of *Stenopterygius quadriscissus* and *Ophthalmosaurus*
 742 *icenicus*, and all of its descendants [node-based] (Fischer *et al.* 2013).

743 **Synapomorphies. Parsimony.** Strongly reduced dentition in adults [129:0→1].

744 **Discussion.** Unexpectedly, *Stenopterygius* is not monophyletic in any analysis (Figs 4, 6, 7),

745 but instead is paraphyletic to Ophthalmosauridae, with *S. triscissus* typically found more
 746 basally than other species of *Stenopterygius*. Where this occurs, this places the occurrence of
 747 the prominent acromion process (one of the defining features of Baracromia; Fischer *et al.*
 748 2013) more basal to the location of this taxon. This character change does occur in the
 749 preferred phylogeny due to the polytomy that includes all species of *Stenopterygius*.
 750 Optimization of characters does suggest that the angular extent increases and the ischium and
 751 pubis fuse completely in Baracromia (Maisch & Matzke 2000), and that the proximal
 752 processes on the femur relatively increase in size (Fischer *et al.* 2013). Additionally, the
 753 relative sizes of the dorsal and ventral humeral processes are increased, although this has
 754 often been associated with Ophthalmosauridae (Fischer *et al.* 2012; Fischer *et al.* 2013). While
 755 these are larger in Ophthalmosauridae, the definition for these characters is non-specific and
 756 so was applied to these non-Ophthalmosauridae Baracromia. Platypterygiinae have been
 757 defined including the large ventral process, with distinct concavities (Fischer *et al.* 2011), and
 758 similarly, Ophthalmosauridae are separated by the plate-like dorsal ridge on the humerus
 759 (Fischer *et al.* 2012) indicating the increased development of this and the musculature
 760 associated with the humerus (Moon & Kirton 2016). In this study, these features of the
 761 humerus have been treated as separate characters, however, if interpreted as a continuum of
 762 humeral development through phylogeny, they could alternatively be treated as a single
 763 multistate character with states, for example: poorly developed humeral processes (non-
 764 Merriamosauria Ichthyosauriformes); developed ventral process (Merriamosauria);
 765 developed dorsal and ventral processes (Baracromia); plate-like dorsal process
 766 (Ophthalmosauridae); well developed, plate-like dorsal and ventral processes
 767 (Platypterygiinae).

Clade **Ophthalmosauridae** Baur, 1887a

Emended definition. All taxa more closely related to *Ophthalmosaurus icenicus* and *Platypterygius hercynicus* than to *Stenopterygius aaleniensis* and *Chacaicosaurus cayi* [stem-based].

Synapomorphies. Parsimony. Humerus with plate-like dorsal ridge [207:0→1]; acute angle at anterodistal humerus [212:0→1].

Discussion. Following Fischer *et al.*'s (2011) emended definition, Ophthalmosauridae would refer to a small clade in consensus-MPT and MLT (Figs 4, 6). To maintain stability in the included taxa, the definition is extended to formally include *Platypterygius hercynicus*– following Fischer *et al.*'s (2012) definitions of Ophthalmosaurinae and Platypterygiinae – and exclude *Stenopterygius aaleniensis* – the immediate sister taxon to Ophthalmosauridae – and *Chacaicosaurus cayi*. While *C. cayi* is here located more basally in Neoichthyosauria in the preferred phylogeny due to lack of resolution (Fig. 7), it has been recovered as the immediate sister taxon to Ophthalmosauridae previously (Fischer *et al.* 2011).

Ophthalmosauridae can be diagnosed by features that include reduction of the extracondylar area of the basioccipital; plate-like dorsal process on the humerus; increased fusion of the ischium and pubis; and loss of notching in the fore and hind limbs (Motani 1999c; Sander 2000; Maisch & Matzke 2000; Fischer *et al.* 2012; Ji *et al.* 2016). However, variability with Ophthalmosauridae reduces the utility of some of these features: the basioccipital extracondylar area is reduced more in Platypterygiinae than in more basal Ophthalmosauridae; similarly, fore limb bone patterns are substantially different between Platypterygiinae than in basal Ophthalmosauridae. These two clades have been separated as sister taxa (Fischer *et al.* 2011; Fischer *et al.* 2012; Fischer *et al.* 2013). Apparent

791 convergences –e.g. the polygonal fore and hind limb elements in more derived
 792 Ophthalmosauridae, the secondary loss of three distal humeral facets in *Cryptopterygius* and
 793 *Nannopterygius*; both convergent with more non-Ophthalmosauridae – complicate the
 794 resolution of this clade, hence a large polytomy in the preferred phylogeny (Fig. 7). Otherwise
 795 prominent features – e.g. the large, plate-like ventral process of Platypterygiinae; the
 796 humerus-intermedium contact in *Aegirosaurus*, *Brachypterygius*, and *Grendelius* – similarly do
 797 not unite taxa that might form a clade. This inconsistency is particularly well shown by the
 798 removal of most Ophthalmosauridae when pruning the consensus-MPT: many taxa are
 799 equally unstable and reduce the resolution present here. Further study of this group may
 800 benefit from selectively removing the least complete taxa alongside those that are equivalent,
 801 however, this may also reduce phylogenetically useful data so was not carried out here.

802 **Discussion**

803 **Ichthyosaur evolution: clades and grades**

804 In reviewing ichthyosaur evolution, Motani (2005) recognized three grades within
 805 ichthyosaur evolution: a basal grade: Early Triassic ichthyosaurs; an intermediate grade:
 806 Middle–Late Triassic ichthyosaurs; and a fish-shaped grade: Late Triassic–Cretaceous
 807 ichthyosaurs. Each of these corresponds to a portion of ichthyosaur phylogeny, represented
 808 by several clades within Ichthyosauriformes, monophyletic or paraphyletic. In the phylogeny
 809 presented here (Fig. 7), the pattern across ichthyosaur evolution is similar. Both the basal and
 810 intermediate grades are paraphyletic with respect to the more derived grades, and identified
 811 by the resolve polytomous nodes. The basal ichthyosaur grade, which includes the basal-most
 812 ichthyosaurians and non-ichthyosaurian Ichthyosauriformes, is marked by the relatively
 813 elongate tail, compared to the trunk, and long propodials and epipodials, compared to the
 814 whole limb, remnants of their terrestrial ancestry (Motani 2005). The metapodials retain the

815 basal hourglass-like form comparable with more basal diapsids (Motani 1999c; McGowan &
816 Motani 2003).

817 In the intermediate grade, most non-parvipelvian ichthyosaurians, there is the gradual
818 acquisition of more fish-like characters: shrinking the size and increasing the number of limb
819 bones to form paddle-like limbs, shortening of the caudal vertebrae, so that the tail becomes
820 shorter relative to the trunk, and the early development of a strong tail bend (McGowan &
821 Motani 2003). This grade may be divided into two subgrades: the earlier, Middle Triassic
822 *Cymbospondylus-Mixosaurus* group, and the Middle–Late Triassic *Shastasaurus-Shonisaurus*
823 group. The former group includes taxa that represent the early ecological diversification of
824 ichthyosaurs, with a broad range of body forms habits, associated with an increase in
825 disparity (Massare 1987; Thorne *et al.* 2011; Fröbisch *et al.* 2013; Dick & Maxwell 2015). This
826 is marked in the above phylogeny by character changes related to the teeth as a potential
827 synapomorphy of Mixosauridae (e.g. character 149:0→1). The more derived members of the
828 intermediate grade than Mixosauridae, which includes traditional ‘shastasaurids’, modify the
829 forelimb further than earlier taxa, particularly through the loss of digits and shortening and
830 rounding of the phalanges (see Online Supplemental Material Document S1.5; Thorne *et al.*
831 2011; Sander *et al.* 2011; Motani *et al.* 2013).

832 The latest, fish-like grade, including all parvipelvians, represent an oft-cited example of
833 convergence with modern pelagic fishes (Motani *et al.* 1996; Motani 2005). While this clade is
834 named for the reduction of the pelvis, this is not an unambiguous synapomorphy (see above
835 and Online Supplemental Material Document S1.6). However, this clade and grade are marked
836 by several changes to the pectoral girdle that affect the form and use of this and the forelimb.
837 Within Parvipelvina, there is a shift between the basal taxa and the clade Baracromia, which
838 has several limb-based character changes towards the node. This marks the later evolution
839 and diversification of this clade and the more derived Ophthalmosauridae that succeeded

840 from the non-baracromian parvipelvian ichthyosaurs in the Middle Jurassic–Cretaceous
841 (Fischer *et al.* 2012; Fischer *et al.* 2013). With the proposal of the above phylogeny, it becomes
842 possible to analyse specific traits, discrete and continuous, across ichthyosaur evolution, and
843 test the reality of the ichthyosaur evolution as a series of grades.

844 **Specimen completeness**

845 The effects of incomplete taxa have often been associated with a lack of characters rather than
846 simply the proportion of missing data (Wiens 2003). Recent metrics to quantify skeletal and
847 cladistic completeness provide comparative methods that may allow attribution of
848 completeness (Mannion & Upchurch 2010). Studies have applied these to several fossil
849 groups, but only recently to marine reptiles (Cleary *et al.* 2015). While specimen
850 completeness is highly variable through the Mesozoic, periods of relatively high
851 completeness – e.g. Hettangian–Toarcian – are coincident with the occurrence of better-
852 resolved regions of the trees presented: approximately Merriamosauria through to
853 Baracromia. Conversely, lower levels of completeness are found in Early–Middle Triassic,
854 Middle Jurassic, and Late Jurassic–Cretaceous taxa, which correspond to the less well resolved
855 portions of the trees: basal ichthyosaurs and Ophthalmosauridae, particularly (Figs 4, 6, 7;
856 Online Supplemental Material Figure S3; Cleary *et al.* 2015). Whether and how skeletal and
857 cladistic completeness of ichthyosaurs is related to phylogeny has yet to be tested.

858 **Phylogeny reconstructions**

859 Throughout the above analyses, the ichthyosaur matrix has been used as an exemplar of a
860 palaeontological dataset: purely morphological data, many taxa are from a few discrete
861 horizons, and completeness varies greatly between taxa. In previous work on ichthyosaur
862 phylogeny, methods of phylogeny inference other than maximum parsimony were limited to

the Bayesian-inference maximum likelihood analyses of Fröbisch *et al.* (2013) and Fischer *et al.* (2016). Simulation data has suggested that Bayesian inference can provide increased accuracy of results over parsimony in palaeontological datasets (Wright & Hillis 2014; O'Reilly *et al.* 2016). However, the importance of missing data and its effect on phylogeny reconstruction is complex (Prevosti & Chemisquy 2010; Wiens & Morrill 2011; Simmons 2012; Sansom 2014). Simulations of data loss have generally focused on formulaic removal, often of a minority of codings – e.g. Wright & Hillis (2014) removed characters with similar rate changes. The present dataset of ichthyosaurs, however, contains over 50% non-coded characters. While these missing data are not purely random, there is a bias towards absence of certain character sets – e.g. small limb bones, limbs, tail vertebrae, and neural spines.

A posteriori analysis and modification of trees – e.g. by pruning – will often provide an increase in resolution and potentially accuracy (Pol & Escapa 2009; Aberer *et al.* 2013). This method has proved useful here as a faster addition to *a priori* STR (Wilkinson 1995; Siu-Ting *et al.* 2015). Previous studies of ichthyosaurs have used an arbitrary proportion of incomplete characters to remove taxa, presenting this alongside the complete analysis (Fischer *et al.* 2013; Fischer *et al.* 2014a). Although this is the simplest method, it does not always prove the best in resolving relationships (Wiens 2003). *A posteriori* identification of unstable taxa allows a determination of the causes of this instability – in the case of PCR pruning by pinpointing conflicting characters (Pol & Escapa 2009) – which provides a useful indication of where the uncertainty lies. This method is preferred as a means of identifying problematic taxa in phylogenetic analyses.

The lack of resolution here between relatively complete taxa – e.g. *Ichthyosaurus*, *Stenopterygius*, and *Temnodontosaurus* within Parvipelvia/Neoichthyosauria – suggests, however, that the characters used to inform the topology are proving inadequate. This may require a reformulation of characters to reflect newer understanding and methodology –

888 likelihood vs parsimony – but most immediately suggests that a thorough revision within a
 889 modern phylogenetic framework is necessary. Posterior samples of trees, however, does not
 890 preclude further study based on phylogenetic inference.

891 The two different topologies found under Bayesian inference imply that different models
 892 support, or resolve, different parts of the tree (Fig. 7; Online Supplemental Material Figure
 893 S3) – i.e. there is rate heterogeneity across the tree, and that different models/priors are
 894 necessary: the posterior distributions found are different to the prior distributions (Online
 895 Supplemental Material Figure S2). This is not surprising, considering that previous studies
 896 have shown that certain parts of ichthyosaur evolution are punctuated by high cladogenesis
 897 rates (Fischer *et al.* 2012; Fischer *et al.* 2013). Stratigraphic correlation of trees also shows the
 898 unevenness present (Motani 1999c; Fröbisch *et al.* 2013). As Bayesian inference has been
 899 shown to be able to recover weak, short branches (Alfaro *et al.* 2003), those clades recovered
 900 around the base of Parvipelvia in this analysis may be confidently recognized, although that
 901 has not been done here. A full investigation of the effects of Bayesian prior selection is beyond
 902 the scope of this study.

903 **Conclusions**

- 904 1. Previous hypotheses of ichthyosaur phylogeny are corroborated, but individual taxon
 905 positions can vary greatly producing topological instability and weak support for
 906 relationships. Ichthyosaurs present a stepwise phylogeny with nested clades separated
 907 by acquisition of characters. Monophyletic groups are present, which can be well
 908 supported, and mark diversification within a particular bauplan – e.g. Mixosauridae
 909 and Shastasauria.
- 910 2. Non-monophyletic genera reaffirm the need for revision of several ichthyosaur taxa,
 911 particularly those based on poor diagnoses and specimens, or phenetic definitions –

e.g. *Temnodontosaurus*, *Mixosaurus* and *Phalarodon*, *Ophthalmosaurus*, *Stenopterygius*, and *Platypterygius*. These issues may be compounded by the variation of form exhibited by several taxa – e.g. *Ichthyosaurus* and *Stenopterygius* – and the wide range of species and specimens available.

3. Unstable ichthyosaur taxa may be the result of inadequate characters as well as inadequate coding (incompleteness). An in-depth, critical re-evaluation of characters may be necessary, particularly for those in the most poorly resolved clades – e.g. basal Ichthyosauriformes, basal Merriamosauria, and Ophthalmosauridae. *A posteriori* identification of unstable taxa and taxon pruning can provide indication of which are inadequately known, and where characters may need revision.
4. Analyses under different phylogeny criteria recover a similar overall topology, but the placement of individual taxa varies greatly, as does consensus resolution. Differences in the resolution of Bayesian inference show that different prior distributions can affect the results, and that a simply distributed prior may not be the most useful.

Supplemental material

Supplemental material for this article can be accessed here:

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1275 Captions

- 1276 **Figure 1.** Previous hypotheses of whole-group ichthyosaur phylogeny. **A**, simplified version of
 1277 Mazin (1982): 51 taxa (excluding *Omphalosaurus*), 14 characters. **B**, Motani (1999c): 27
 1278 ingroup taxa, 105 characters, parsimony analysis. **C**, Sander (2000): 16 ingroup taxa, 120
 1279 characters, parsimony analysis. **D**, Maisch & Matzke (2000): 32 ingroup taxa, 128 characters,
 1280 parsimony analysis. **E**, Fröbisch *et al.* (2013): 32 ingroup taxa, 112 characters based upon
 1281 Sander *et al.*'s (2011) modification of Motani (1999c), Bayesian-inference likelihood

1282 analysis.



1283

Figure 2. Examples of previous hypotheses of ichthyosaur subclade relations. **A**, Nicholls and Manabe's (2001) Shastasauria phylogeny: 14 taxa, 44 characters. **B**, Jiang *et al.*'s (2006) Mixosauridae phylogeny: 9 taxa, 23 characters. **C**, Fischer *et al.*'s (2013) Parvipelvnia phylogeny: 26 taxa, 66 characters, **D**, Fernández's (2007) Thunnosauria phylogeny: 9 taxa, 24 characters. **E**, Druckenmiller and Maxwell's (2010) Thunnosauria phylogeny: 16 taxa, 49 characters. All used parsimony analysis in PAUP* or TNT.

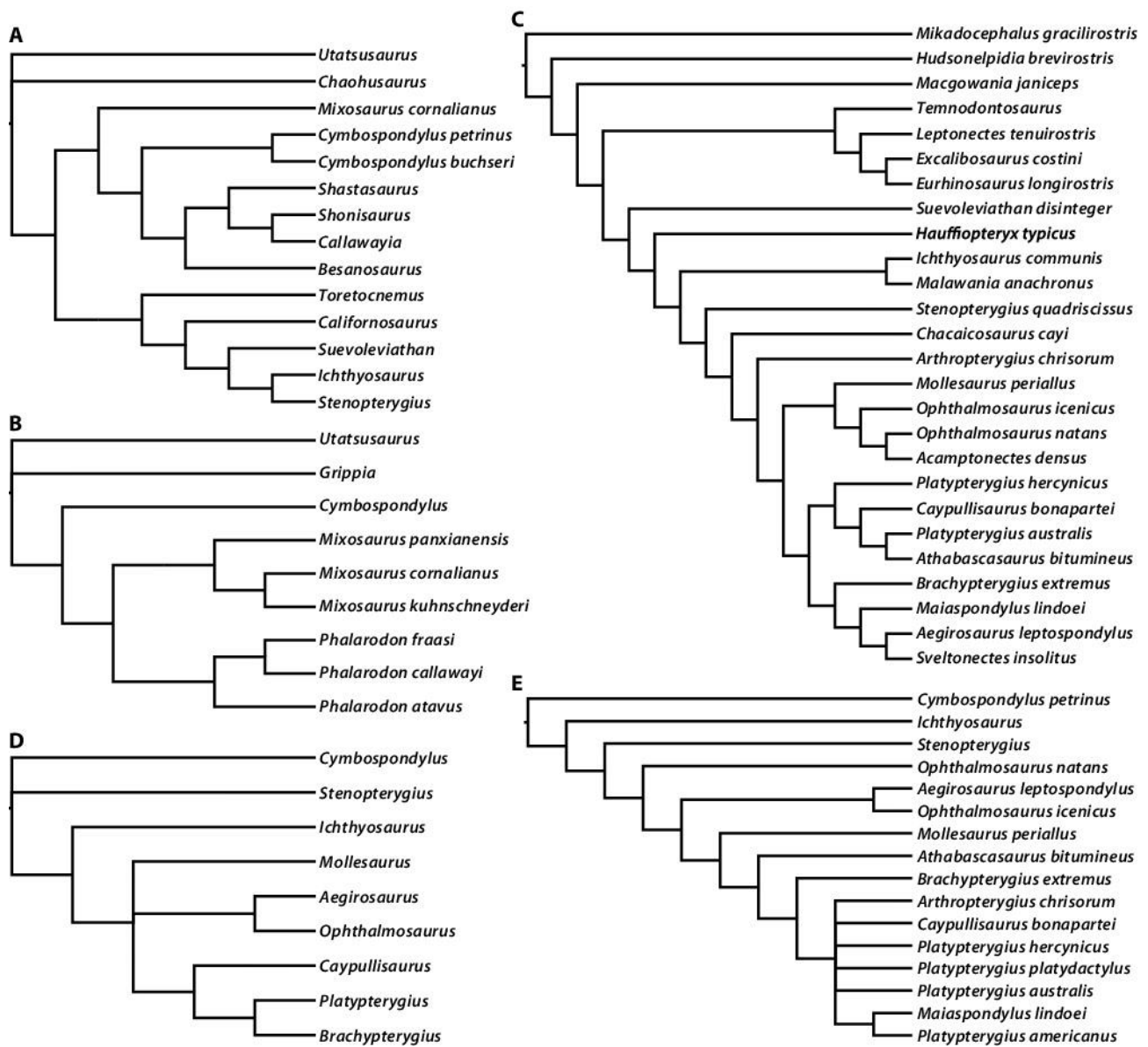
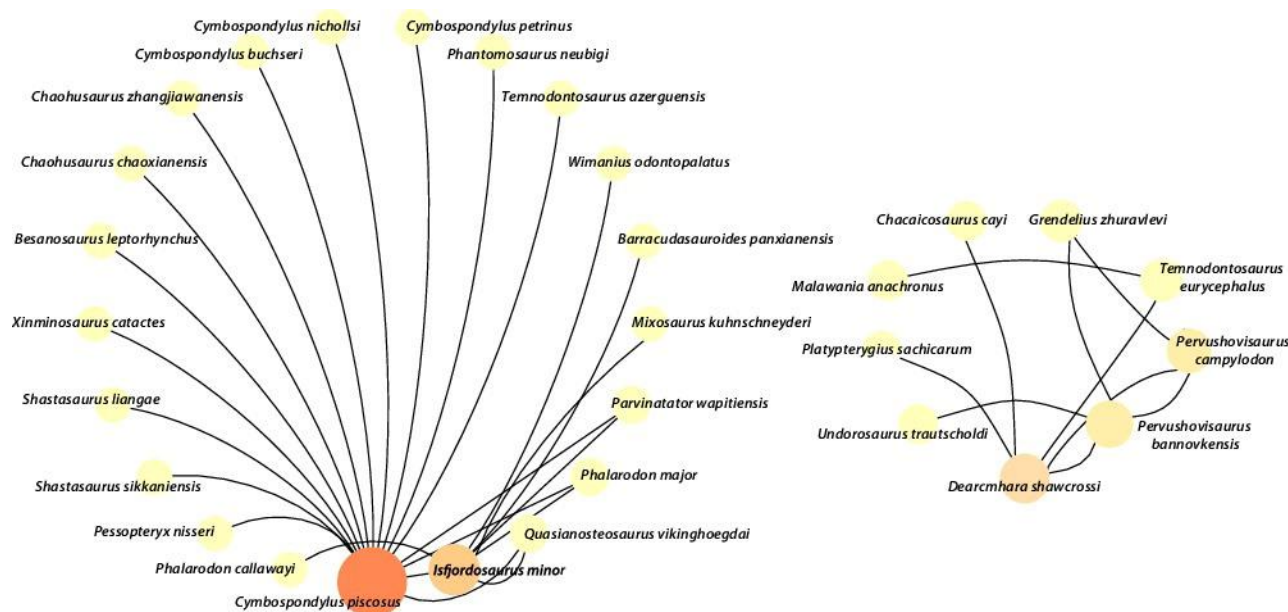


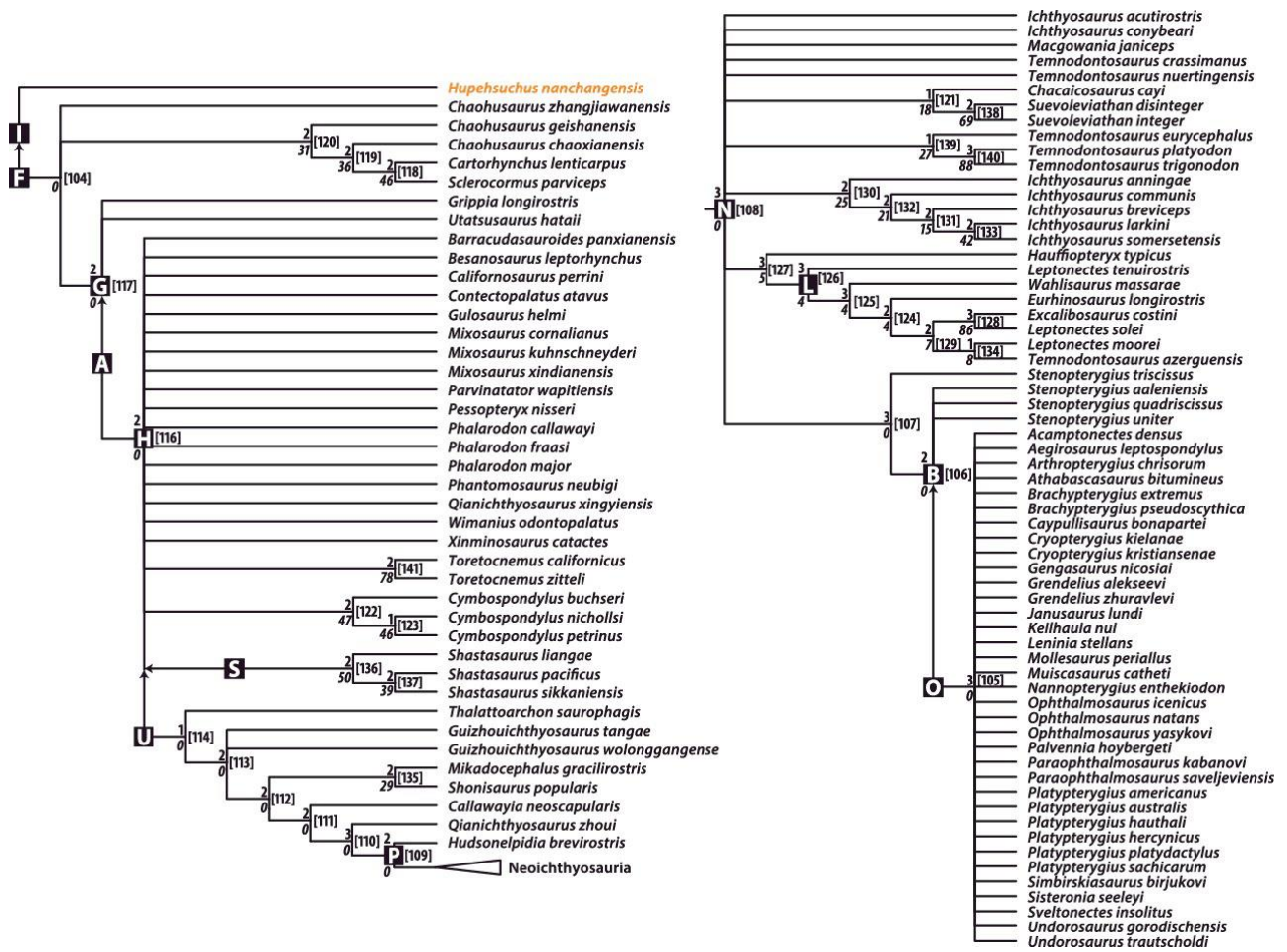
Figure 3. Resultant networks from Concatabomination analysis showing the more problematic taxa (larger, redder circles) and their similarity to other, less problematic taxa (smaller, yellow circles). *Cymbospondylus piscosus*, *Dearcmhara shawcrossi*, *Isfjordosaurus minor*, and *Pervushovisaurus bannovkensis* are identified as the taxa with most redundancy. Other, unconnected taxa and self-referential similarity are not shown.



1298

Figure 4. Strict consensus of 11,536 recovered MPTs recovered from equal weights parsimony analysis in TNT with 104 OTUs: 1666 steps, CI = 0.150, RI = 0.521, RCI = 0.0782. Support values given are: decay index above the branch in roman type, symmetrical resampling per cent below the branch in italic. Named and discussed clades are labelled; node numbers are indicated in square brackets: **A**, Ichthyosauria; **B**, Baracromia; **H**, Hueneosauria; **I**, Ichthyosauriformes; **L**, Leptonectidae; **N**, Neoichthyosauria; **O**, Ophthalmosauridae; **P**, Parvipelvia; **S**, Shastasauria; **U**, Euichthyosauria. Node-based clades are indicated at the node; branch-based clades are indicated with an arrow towards the base of the clade. Outgroup taxon is indicated in orange. See also Online Supplemental Material Figures S1 &

1308 S2.



1309

1310 **Figure 5.** Visualisations of uncertainty in the 11,536 recovered MPTs from equal weights
 1311 parsimony analysis in TNT with 104 OTUs (see also Fig. 4). **A**, cluster network showing
 1312 relationships supported by at least 25% of MPTs; teal edges indicate uncertain relationships.
 1313 **B**, consensus network of branches supported by at least 25% of MPTs; distances (branch
 1314 weights) represent mean support for relationships; for clarity, not all taxa are labelled.
 1315 Outgroup taxon is indicated in orange. See also Online Supplemental Material Figures S1 & S2.

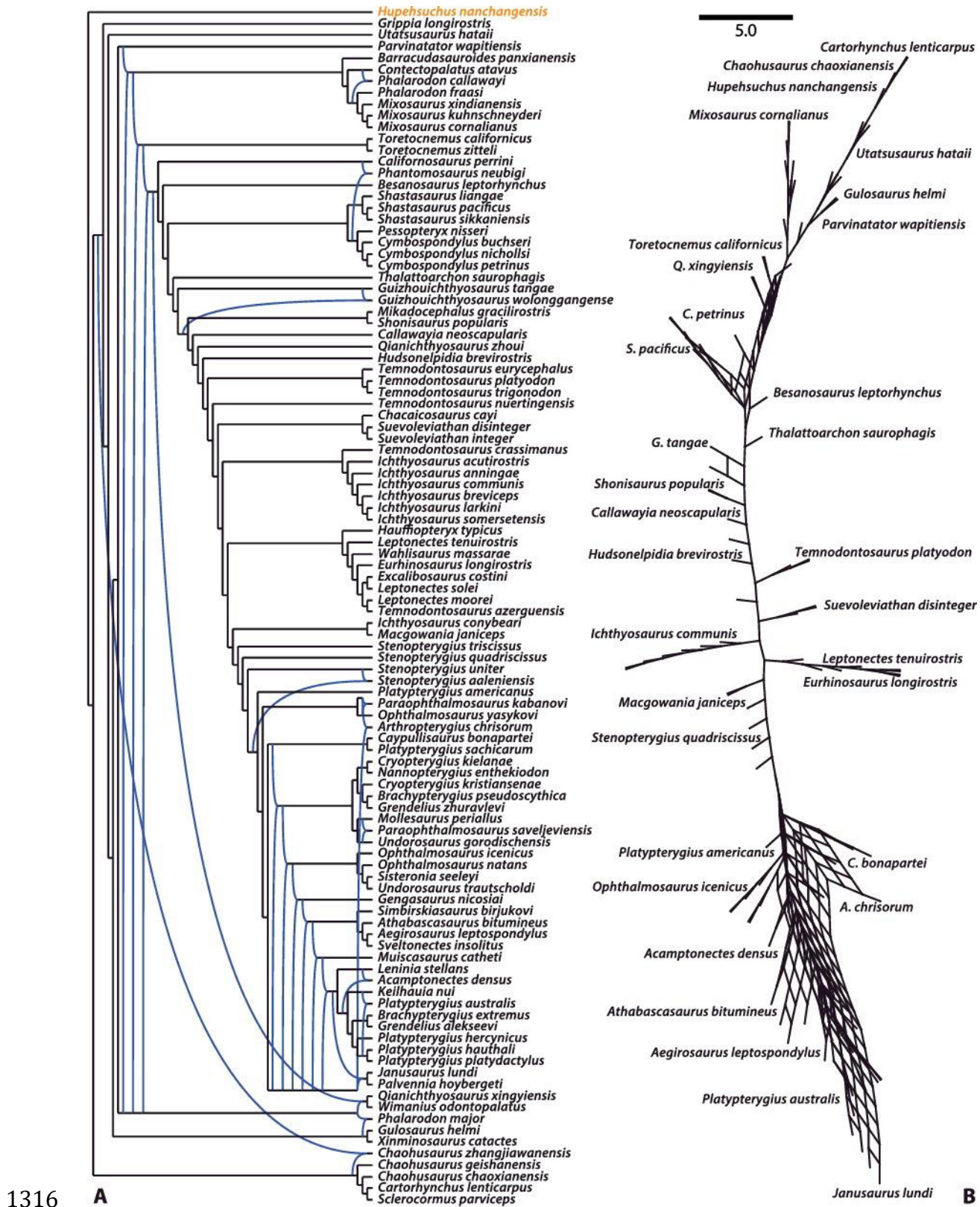


Figure 6. Most likely tree recovered from analysis in RAxML with 104 OTUs. Bootstrap supports from 2000 replicates are indicated below each branch. Branch lengths are scaled to the substitutions along each branch; scale represents 0.2 substitutions. Named nodes are

indicated as in Fig. 4 with the addition of **M**, Merriamosauria; **T**, Thunnosauria; **X**,
 Mixosauridae. Outgroup taxon is indicated in orange.

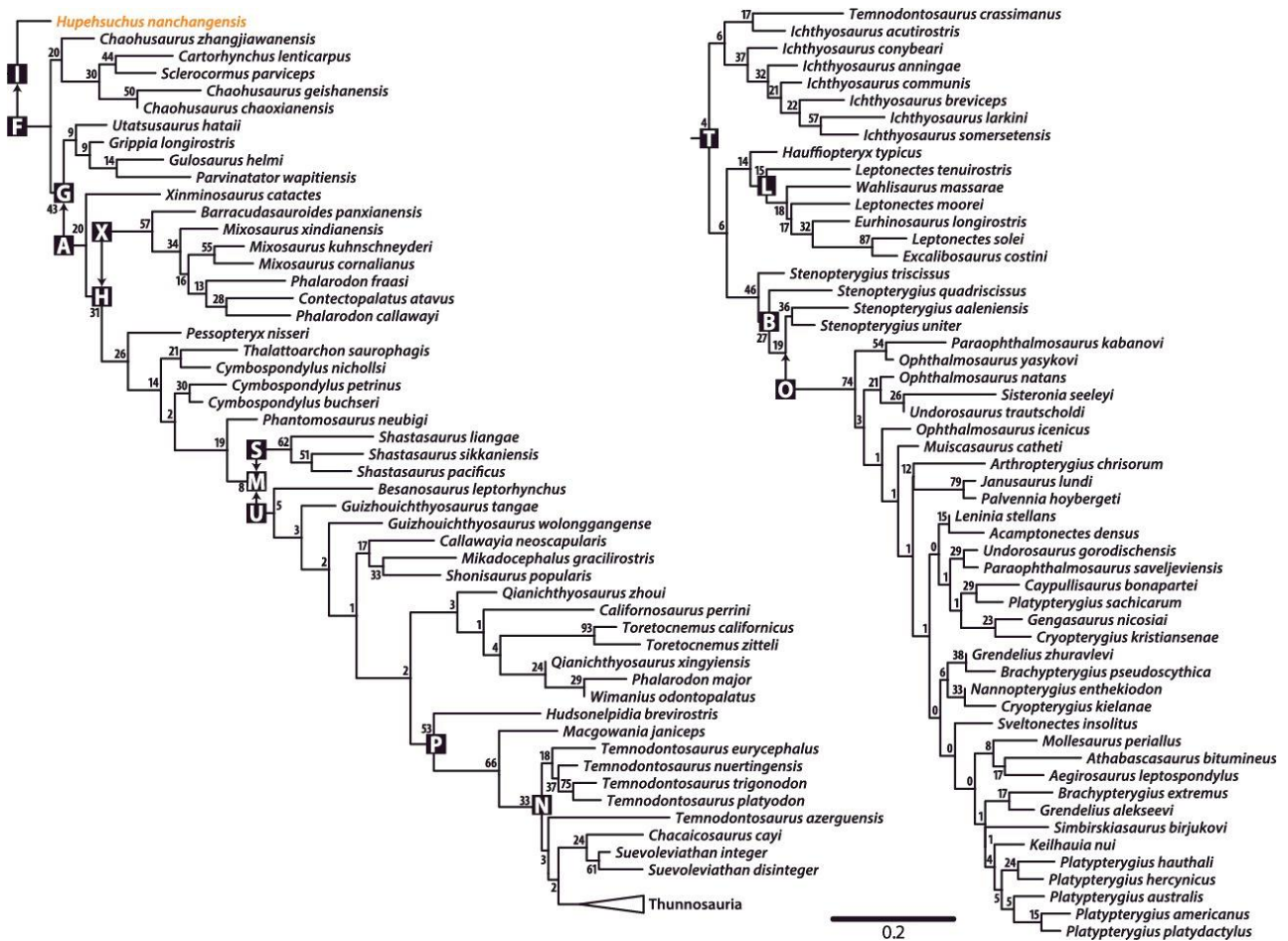
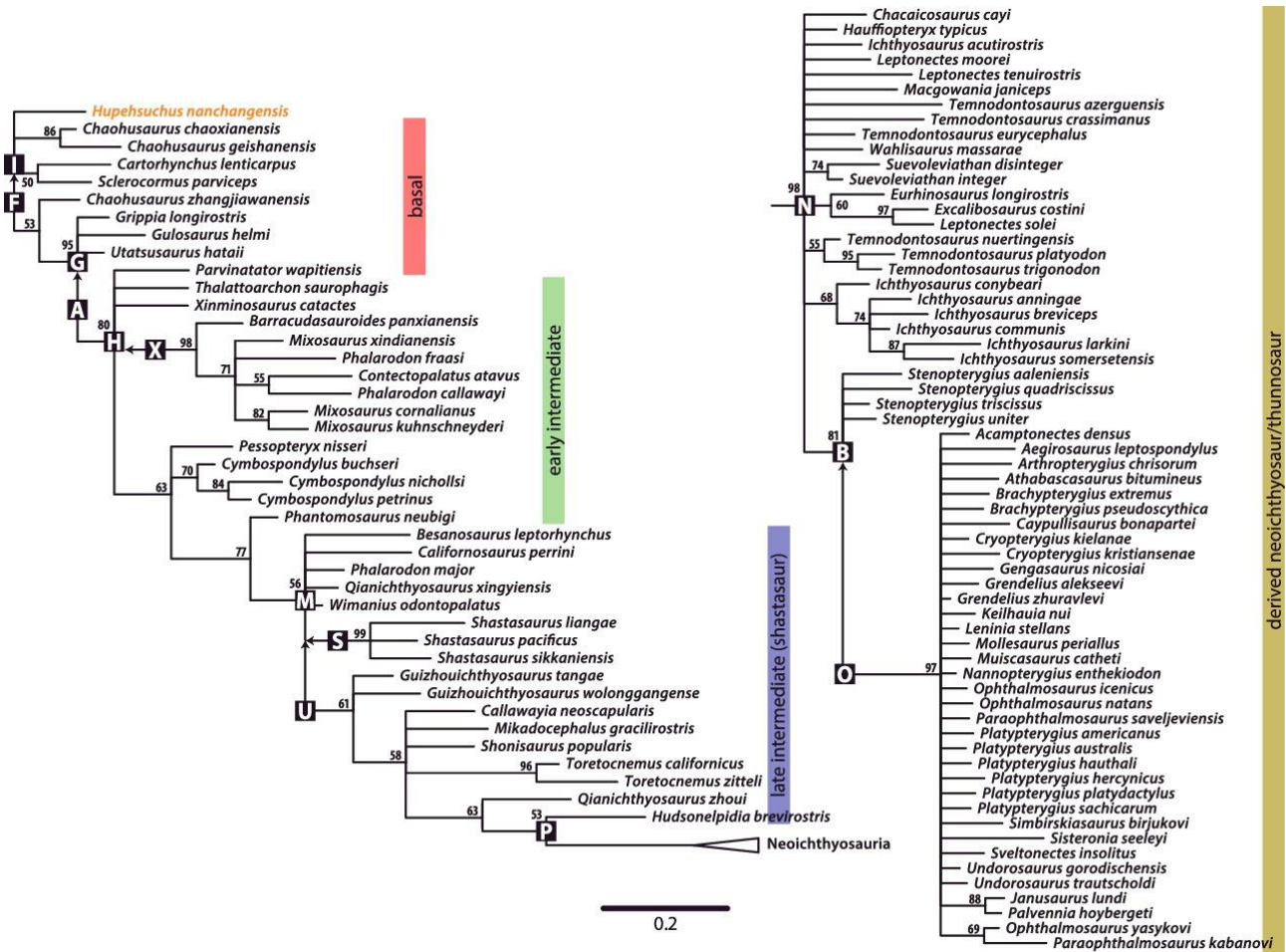


Figure 7. Resultant 50% majority rule consensus tree of 24,710 sampled trees from Bayesian inference analysis in MrBayes using a gamma-distributed site rate variation with 104 OTUs. This is the preferred tree. Clade credibility values are shown to the right of each node. Branch lengths are scaled to the substitutions along each branch; scale represents 0.2 substitutions. Named clades are indicated as in Fig. 4. Outgroup taxon is indicated in orange. Grades are shown by coloured bars. See also Online Supplemental Material figures S3, S4.



1329

1330 **Figure 8.** Visualisations of uncertainty in 24,710 sampled trees from Bayesian inference
 1331 analysis with a gamma-distributed site variation prior in MrBayes with 104 OTUs (Fig. 7). **A**,
 1332 cluster network showing relationships supported by at least 25% of sampled trees; teal edges
 1333 indicate uncertain relationships. **B**, consensus network of branches supported by at least 25%
 1334 of sampled trees; distances (branch weights) represent mean support for relationships; for
 1335 clarity, not all taxa are labelled. Outgroup taxon is indicated in orange.

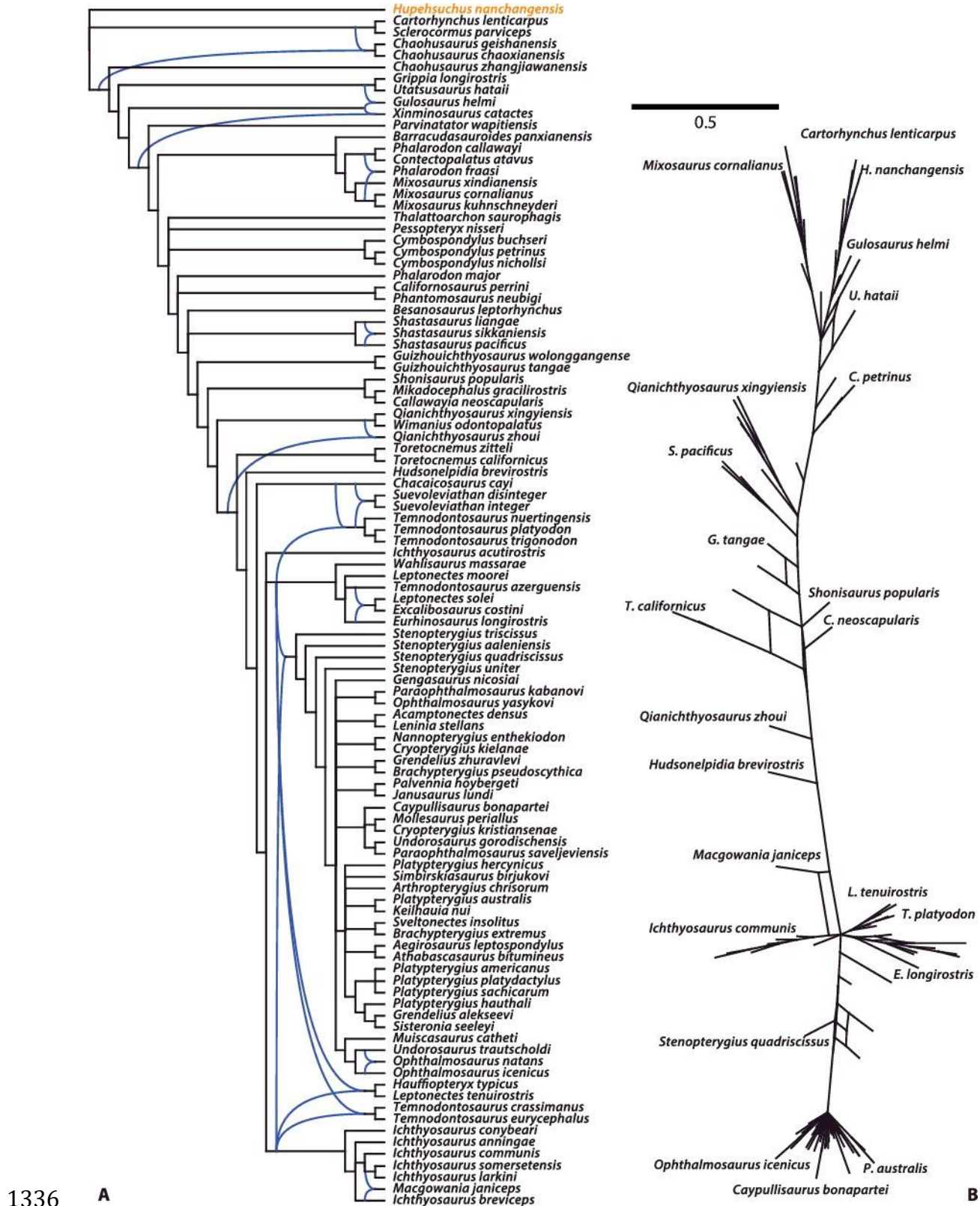
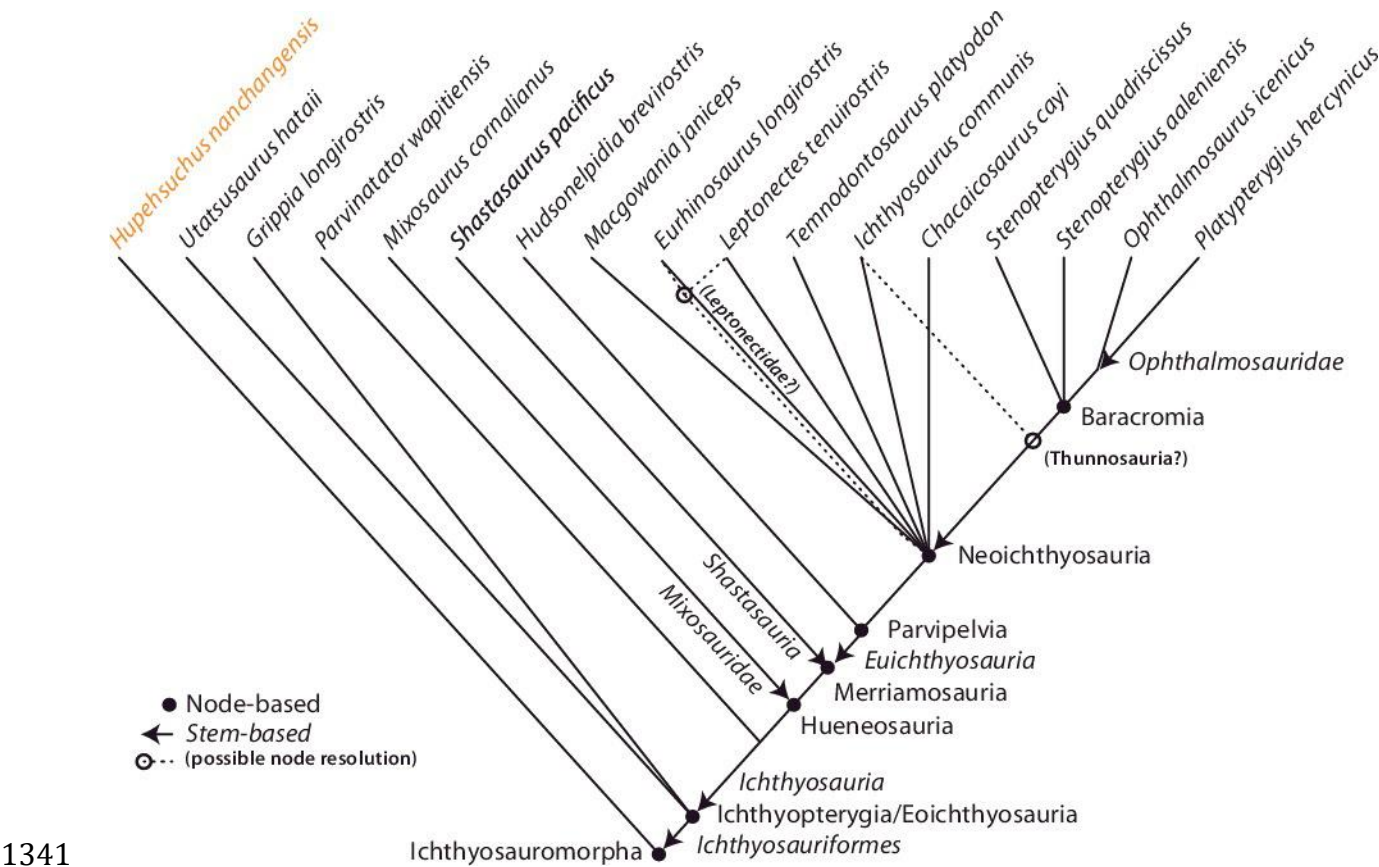


Figure 9. Summarised clad definitions for resolved (solid lines, filled circles) and possible (dashed lines, unfilled circles) clades taken from the preferred phylogeny (Fig. 7). Only

1339 defining taxa are shown. Uncertain clade positions are shown in brackets. Node-based names
1340 are in upright font; stem-based names are in italic font. The outgroup is indicated in orange.



1342 **Table 1.** Taxa pruned by PCR analysis from the strict consensus of 11,536 MPTs recovered
1343 under equal weights TNT analysis with 104 OTUs. The polytomous node in strict consensus
1344 (Fig. 4) from which each taxon is pruned is indicated, alongside the coded character
1345 completeness (%). See also Online Supplemental Material Document S4 and Figure S2.

Node	Taxon	Completeness (%)
105	Acamptonectes densus	41.8
Â	Aegirosaurus leptospondylus	64.5
Â	Arthropterygius chrisorum	22.6
Â	Athabascasaurus bitumineus	33.1
Â	Brachypterygius extremus	55.7
Â	Brachypterygius pseudoscythica	27.9
Â	Caypullisaurus bonapartei	58.9
Â	Cryptopterygius kristiansenae	59.6
Â	Crypterygius kielanae	26.8

Â	Grendelius zhuravlevi	15.3
Â	Grendelius alekseevi	46.7
Â	Leninia stellans	26.8
Â	Mollesaurus periallus	34.5
Â	Muiscasaurus catheti	27.2
Â	Nannopterygius enthekiodon	31.7
Â	Ophthalmosaurus icenicus	96.5
Â	Ophthalmosaurus natans	77
	Paraophthalmosaurus	
Â	saveljeviensis	28.9
Â	Platypterygius americanus	58.2
Â	Platypterygius sachicarum	23.3
Â	Simbirskiasaurus birjukovi	18.5
Â	Sisteronia seeleyi	16.4
Â	Sveltonectes insolitus	69.3
Â	Undorosaurus gorodischensis	40.8
Â	Undorosaurus trautscholdi	17.1
108	Ichthyosaurus conybeari	73.2
Â	Macgowania janiceps	38.3
Â	Temnodontosaurus nuertingensis	25.8
115	Californosaurus perrini	35.5
Â	Phalarodon major	6.6
Â	Xinminosaurus catactes	35.5
Â	Node 136 (Shastasauria)	Â
Â	Node 114 (Euichthyosauria)	Â